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The BOTANICAL GAZETTE

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Volume LXXXV Number 4

THE BOTANICAL GAZETTE

A JOURNAL EMBRACING ALL DEPARTMENTS OF BOTANICAL SCIENCE

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BOTANICAL GAZETTE

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STUDIES OF PLANTS IN THE BLACK HILLS OF SOUTH DAKOTA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 380

HERMAN E. HAYWARD

(WITH FIFTEEN FIGURES)

Purpose and scope of study

The Black Hills of South Dakota have for many years extended an attraction because of their unique geographical position, suggesting as it does hidden possibilities of interesting floral situations and associational relationships. The present study has grown out of an increasing desire to investigate the situation at close range, and to study the flora from the floristic and successional points of view.

The region was first visited during the summer of 1926, and six weeks were devoted to a preliminary reconnaissance. This resulted in a decision to attack the problem from two angles, floristic and formational. The intermixture of northern, southern, western, and eastern elements in the flora seemed of sufficient interest to justify a floristic analysis. The results of this phase of the survey constitute part I of this paper. The study dealing with the plant formations was carried on during the summer of 1927, the field work extending from June 8 to August 15. During this time studies were made of habitats that had been selected as a result of the field work of 1926 (fig. 1). Part II embodies an analysis of the plant formations thus determined.

Geography and topography

The Black Hills are located in southwestern South Dakota and eastern Wyoming, extending from latitude 43° 15′ to 44° 30′ N., and

from longitude 103° 10′ to 104° 20′ W. (fig. 2). The length of the higher portion of the uplift is about 100 miles and it is 50 miles across at its greatest width. Of a total area of about 4500 square

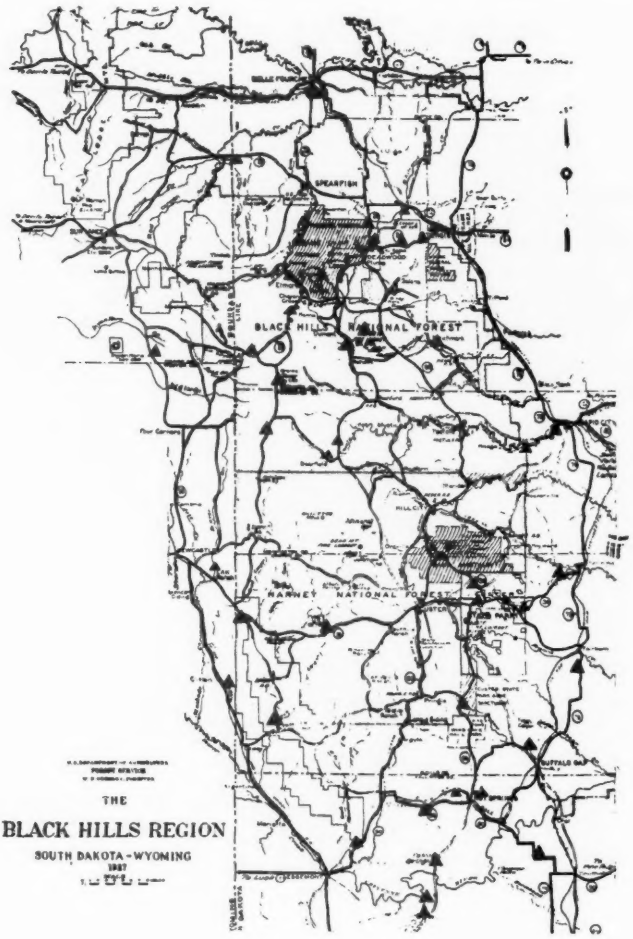

FIG. 1.—Black Hills region; black triangles indicate points at which studies were made.

miles, approximately two-thirds are in South Dakota, while one-third is in Wyoming.

The Black Hills rise several thousand feet above the adjacent plains, whose elevations range from 2500 feet near Belle Fourche and 3000 feet near the Cheyenne River, to 3300 or 3500 feet at the

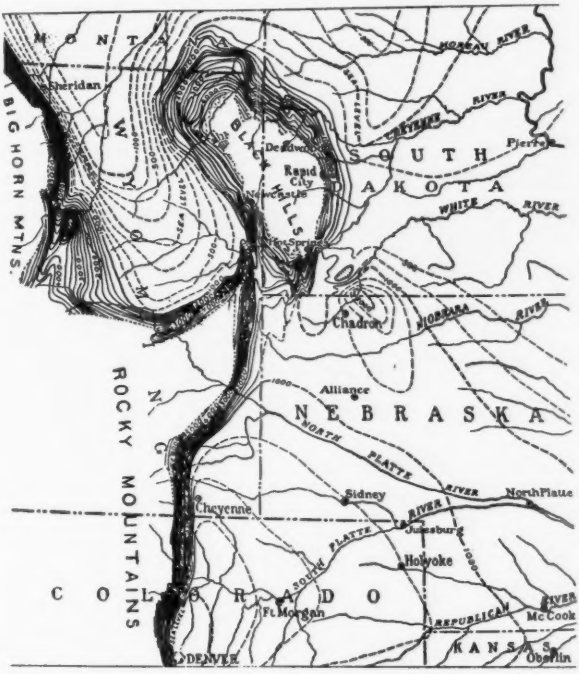

FIG. 2.—Black Hills, showing their geographical position

outer edge of the Hogback Ridge. The highest point in the Hills is Harney Peak, with an elevation of 7242 feet.

The topography (fig. 3) has been so clearly described by DARTON (8) that it can best be presented by giving a condensed summary of his account. The four outstanding features are the Hogback Ridge, the Red Valley, the Limestone Plateau, and the central area.

The Hogback Ridge forms the outer rim of the Hills, completely

encircling them. For the most part it consists of a single ridge of hard sandstone, which presents a steep face toward the Red Valley, and rises abruptly several hundred feet above the bottom of the valley, to an elevation of 3800 feet near Rapid City, and 4900 feet

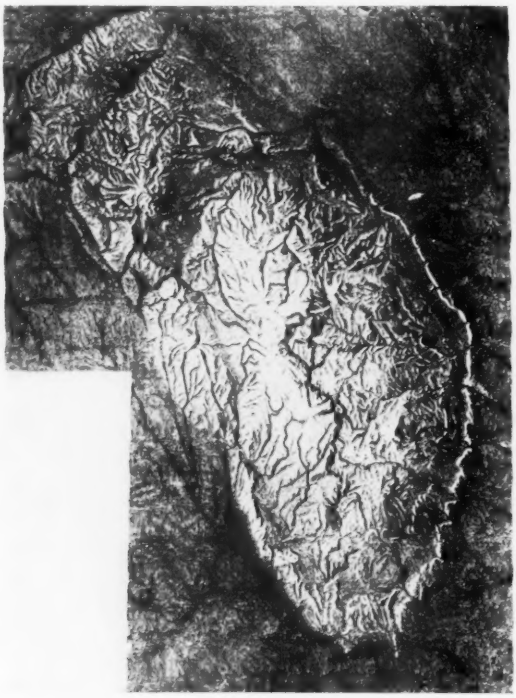

FIG. 3.—Topographic map of the Black Hills showing Hogback Ridge, Red Valley, Limestone Plateau, and central hills.

at Elk Mountain. The outer side slopes gradually down to the plains. It is cut at numerous places by gaps, through which the streams arising in the hills pass out to join the waters of the Cheyenne and Belle Fourche rivers.

The Red Valley extends almost continuously around the Black Hills, and is one of the most striking features of the region because of the red color of its soil and the absence of trees. Its outer side is

the steep inner face of the Hogback Ridge previously mentioned, while its inner side consists of fairly steep limestone slopes. It does not exceed 2 miles in width, and in some places is much narrower, due to the steep dip of the strata. The altitude of the valley along the east side is 3300–3500 feet.

The Limestone Plateau is an interior highland belt within the Red Valley, ranging 2–15 miles in width. The western portion, which is broader than the eastern, slopes gently downward to the Red

FIG. 4.—Rim of Limestone Plateau as seen from east near Castle Creek

Valley, but its eastern or inner side is lined by abrupt cliffs that rise in places 800 feet above the central valleys (fig. 4). The plateau is higher than a large portion of the central area, attaining an altitude of 7100 feet at Crooks Tower, and thus forming the main divide of the Black Hills. South of the headwaters of Beaver Creek the plateau swings toward the eastern side of the Hills, where it is much narrower than on the western side, forming a ridge with a steep western face that reaches altitudes ranging from 5000 to 6600 feet. Streams arising at the higher altitudes of the western plateau have cut deep canyons in the limestone, and, after crossing the central region of crystalline rocks, have cut their way through the eastern ridge and joined the Cheyenne River.

The central area includes scattered rocky ridges and mountain peaks lying within the encircling limestone area. Most of these range from 5000 to 6600 feet in height, although several peaks are approximately 7000 feet, and the granite crags of Harney Peak exceed that figure (fig. 5). Throughout this area are parklike valleys, the wider ones being at the heads of canyons that extend outward to the northeast, east, and south.

FIG. 5.—The Needles in central hills near Harney Peak, habitat of *Pinus flexilis*

Drainage

The Black Hills lie between the Belle Fourche and the Cheyenne rivers. The former, running northeastward from its source in Wyoming, makes an abrupt turn near the Montana-Wyoming line north of the Bear Lodge Mountains, flows in a southeasterly direction to Belle Fourche, and ultimately joins the Cheyenne about 50 miles east of Bear Butte (fig. 6). The Cheyenne River skirts the southern foothills, swings northeastward to its junction with the Belle Fourche, and finally empties into the Missouri River. From the watershed of the Limestone Plateau, Red Water and Inyankara creeks flow northwest into the Belle Fourche River; while Beaver Creek flows south, joining the Cheyenne at Edgemont. The eastern watershed is more plentifully supplied with streams. Spearfish and Whitewood creeks flow northeastward to join the Belle Fourche.

Elk, Boxelder, Rapid, Spring, and French creeks, together with Fall River, flow into the Cheyenne.

The erosive action of these streams has resulted in deep canyons whose sheer walls rise many hundreds of feet. The most notable of these is Spearfish Canyon, which is more than 1000 feet deep. It is in these northern canyons that the greatest degree of mesophytism is found, many of them being rich in moisture-requiring ferns and herbs.

FIG. 6.—Bear Butte: one of the Tertiary igneous intrusions characteristic of the northern hills.

Climate

The climate[1] is characterized by late spring rains, summers that are hot and relatively dry, and cold winters with a moderate snowfall. The mean annual temperature for five stations, Deadwood, Fort Meade, Hermosa, Rapid City, and Spearfish is 45.6° F., while the midsummer average for the same stations is 70°. There is a great daily range of temperature in the summer, the days being

[1] The figures given in the section on climate were compiled from summaries of climatological data for the United States for sections 25 and 33 up to 1920 inclusive, and from annual and monthly reports from that date up to September 1, 1927. See also DARTON (8).

very hot at midday and the nights invariably cool. Winter temperatures for the same stations in January average from 22° to 25°.

In the central hills at the higher elevations, frosts begin early in the fall and continue until very late in the spring. At Deadwood the average length of the growing season is only 107 days, from May 31 to September 15, and it is not uncommon for frosts to occur as late as the middle of June and as early as August. In the eastern foothills the growing season is considerably longer than in the western, three stations in the former averaging 141 days, as compared with an average of 113 days for the same number of stations in the latter.

The most striking feature of the climate is the extreme variability of the precipitation from year to year at a given station, and from place to place in a given year. Thus Rapid City had 25.10 inches in 1923 and 14.91 inches the following year, and Lead had 16.49 inches in 1921 and 35.36 inches in 1922. The average annual precipitation in 1926 for fourteen stations within the Black Hills region was 20.97 inches; but the range of precipitation at the several stations varied from 14.67 inches at Belle Fourche to 38.26 inches at Harvey's Ranch in the central hills.

On the basis of complete figures for twenty-one stations, May and June are the months of greatest precipitation, the latter slightly exceeding the former. The combined rainfall of the two months is 30 per cent of the total annual figure. Nearly 60 per cent of the precipitation occurs during the growing season, from May to September inclusive.

The northern hills have the greatest rainfall. Five stations give an average of 24.45 inches, as compared with 21.34 inches at four stations in the central hills. The foothills are much drier, the average annual rainfall for ten stations being 18.25 inches. The Black Hills receive appreciably more moisture than the surrounding plains. Figures for South Dakota, west of the Missouri River and exclusive of the stations in the Black Hills, show an average annual precipitation of 17.21 inches; and northeastern Wyoming east of the Big Horn Mountains has only 15.73 inches.

It is evident from the foregoing that precipitation is one of the most important factors in the interpretation of the plant life, since

there are so many significant variations in the rainfall. Total precipitation in the Black Hills as a unit is of no value in studies of plants in this area, and it is necessary to consider each habitat separately in dealing with this factor.

Geologic history

Probably no other region in the United States has received more careful attention from the geologist than the Black Hills. The reason for this is twofold. From the purely scientific standpoint, they afford one of the most complete and understandable pictures of past geologic processes to be found in western United States. The situation is almost diagrammatic in its major details. As WARD (30) states: "The Black Hills are an object lesson in geology." On the other hand, the discovery of gold in the hills led to a much more careful study of this region than is accorded to one lacking in valuable mineral deposits. It is not necessary, therefore, to do more than indicate briefly the record of major geologic events.[2]

The story of the making of the Black Hills is one of alternating epochs of submergence with accompanying deposition, followed by periods of uplift with resulting erosion and planation. Thus in pre-Cambrian times, the record indicates deposition of sedimentary materials on the floor of a sea, followed by a period of igneous activity which resulted in the granite intrusions that now form the central granite core of the Harney region. During the period of Cambrian submergence it is probable that the Black Hills, like the Big Horn Mountains to the west, formed an island in this great inland sea. The record of Ordovician-Devonian time is extremely meager, being represented only by the Upper Ordovician Whitewood limestone, which is found in the northwestern portion of the Black Hills. In the Carboniferous there was again a period of submergence that extended over the greater portion of the Rocky Mountain province. The early Mississippian seas laid down calcareous sediments, and in later Carboniferous (Pennsylvanian) time much fine sand was deposited. Then followed uplift, and the accumulation of

[2] For a bibliography of the geologic work done in the Black Hills, see O'HARRA, C. C., South Dakota School of Mines, Bull. 11. 1917; also DARTON, N. H., and PAIGE, SYDNEY, U.S. Geol. Sur., Folio no. 219. 1925.

the lower red beds of the Opeche formation of probable Permian time.

Widespread submergence is again indicated by the deposition of the thin Minnekahta formation by sea water, and then came a continuance of the red bed deposition which was laid down by shallow salty lakes. Extensive uplift took place in Triassic and Jurassic time, followed by cycles of submergence and uplift in Cretaceous time, with the accompanying deposition of various sandstones and shales. In Tertiary time the Black Hills dome was uplifted to a considerable height; and, by the Oligocene epoch, the principal topography as now existent was established. In connection with this general uplift, it is probable that the igneous intrusions that are so common in the northern hills took place (fig. 6).

Continued mountain growth occurred after the Oligocene, and this was followed by extensive erosion. If there were deposits of Miocene and Pliocene formations, they must have been removed by subsequent erosion, as no representatives of these epochs have been found in the region. The Quaternary shows evidence of some additional uplift, as well as widespread erosion which removed many of the preceding deposits.

Glaciation

There is no evidence of glaciation in the Black Hills, and it is probable that plant life continued to exist there during glacial time. The glacial epoch must have affected the climatic conditions of the region profoundly, however, and it is therefore pertinent to note the proximity of the glacial area of the Wisconsin age.

According to UPHAM (**26**), the Dakota lobe of the Wisconsin ice sheet "from its junction with the Minnesota lobe near the head of the Coteau des Prairies, 25 miles west of Lake Traverse and Brown's Valley, at first reached about 200 miles south along the valley of the James or Dakota River to Yankton and the Missouri." Its western margin approximated the present course of the Missouri River, swinging northward across the state of South Dakota into central North Dakota, and thence westward across northern Montana. The edge of the glacial ice sheet at its greatest extent, therefore, was approximately 150 miles from the Black Hills.

There is evidence of local glaciation in the Big Horn Mountains.

which lie 100 miles west of the Hills. SALISBURY (**23**) states: "the Big Horn Mountains were occupied by glaciers during two widely separated glacial epochs." An area of about 300 square miles was covered with moving ice; and, at the time of maximum glaciation, it is probable that there was an almost continuous area of ice and snow over a region 40 miles long and 27 miles wide. This glaciation has been referred definitely to the last glacial epoch.

History

1. PERIOD OF EARLY EXPLORATION.—Early accounts of the Black Hills deal chiefly with general descriptions of the country traversed. They emphasize the topographic, geologic, and humanistic features, but contain little of scientific value concerning the plant life of the region. In 1803 the first governmental expedition into the northwest was organized, under the leadership of Captains LEWIS and CLARK. This expedition did not visit the Black Hills, but referred to them in their report.

In 1810 the HUNT expedition left the Missouri River, and traveled overland on a journey to Astoria near the mouth of the Columbia River, probably traversing a part of the Black Hills. The discovery of mammalian remains in the Bad Lands of the White River country resulted in a series of expeditions into that region.

2. PERIOD OF MILITARY EXPLORATION.—In 1855 the Sioux expedition into the Dakota country was made under the command of General W. S. HARNEY, and in the accompanying geological report HAYDEN makes several references to the flora of the region. Further explorations by WARREN and HAYDEN were carried on in 1857, when they practically encircled the Hills. HAYDEN again visited the Hills in 1859, as the geologist in the expedition led by RAYNOLDS (**21**), to explore the region of the Yellowstone River and its tributaries. In the report of his geological findings (**12**), which he presented in 1861, there is a list of the flora of the upper Missouri region, prepared by GEORGE ENGELMANN, which is probably the first taxonomic work referring to the Black Hills. A list of 721 plants is reported, with approximate ranges in some instances, and the points of collection in others. Of these, 34 are specifically referred to the Hills, and 76 are noted as species from the Bad Lands.

In 1874 CUSTER (7) organized an expedition at "Fort Abraham Lincoln, Dakota Territory for the purpose of reconnoitering a route from that post to near Bear Butte in the Black Hills, and exploring the country south, southeast and southwest of that point." This expedition is of particular interest, as it was the first one to penetrate the interior of the region. DONALDSON, the botanist of the expedition, estimated the number of flowers in bloom in Floral Valley at 50, while an equal number of varieties had bloomed or were yet to bloom. The number of trees, shrubs, and grasses was estimated at 25, making a total flora of the valley embrace 125 species. LUDLOW (13) accompanied the CUSTER expedition as engineer officer. His report includes two lists of plants, which are the first that can definitely be related to the Hills proper. The first, a list of the trees and shrubs, was compiled by N. H. WINCHELL, and contains the names of 36 species. In it *Pinus resinosa* Ait. is erroneously listed as the only species of pine in the region. The second list includes the names of 75 plants, representing 23 families, which were collected by DONALDSON and determined by JOHN M. COULTER.

Reports of gold following CUSTER'S expedition caused the government to send a geologic survey into the Hills the following year. This party was in the field for nearly five months, and made a careful survey of the entire area between the forks of the Cheyenne. JENNEY (18) was particularly impressed with the luxuriant growth of the grasses, the abundant timber, and the large number of wild fruits. He observed that the eastern aspect of the flora "bears quite a resemblance to that of southern Maine and New Hampshire in the same latitude." Although this expedition was primarily a geologic and topographic survey, a number of plants were collected and later determined by ASA GRAY. The NEWTON-JENNEY report (18) includes a list of 174 plants.

3. RECENT BOTANICAL STUDIES.—In 1892 RYDBERG was commissioned by the United States Department of Agriculture as an agent in the Division of Botany, for the purpose of making an investigation of the flora of the Black Hills. Prior to this time, such botanical work as had been done was purely incidental, and no serious attempt had been made to make an accurate survey of the

flora. The party spent nearly three months in the field and collected throughout the Hills.

In this report RYDBERG (**22**) divides the Black Hills into five floral districts: Foothills, Minnekahta Plains, Harney Mountain Range, Limestone District, and Northern Hills. Each district is discussed from the floristic standpoint, and the characteristic plants are noted with comments upon their ecology, geographic relationships, and taxonomic characters. The report contains a list of 688 species, representing 82 families, with data regarding the collection of each.

In 1895 WILLIAMS (**31**) published a list of trees and shrubs native to South Dakota, which included plants from the Black Hills. In 1898 BESSEY visited the Hills and investigated the occurrence of *Adiantum capillus-veneris* at Cascade. He concluded that it had not been introduced by human agency, but that it is indigenous along this warm stream. In 1899 SAUNDERS (**24**) published a catalogue of the ferns and flowering plants of South Dakota, which includes 508 species of Black Hills plants, and 144 others that might be referred to that region on the basis of the general range given, a total of 652 plants.

Since 1900 there have been several brief articles citing additions to the flora. VISHER (**27–29**) visited the Hills in 1908, 1911, and 1912, and made collections on each occasion. His published lists of additions to the flora include the names of 115 plants. In 1915 BALL (**2**) published an account of the willows of the Black Hills which summarized the results of personal collections made in 1908, 1910, and 1913. He lists 12 species of native willows, 3 of which range nearly across the continent. One is a distinctly eastern form, the Black Hills being its western limit; while 8 are western species, typical of the Rocky Mountains and westward, that have their eastern limits in the Hills.

In 1923, OVER (**19**) published a list of the trees and shrubs of South Dakota which gives the names and ranges of 85 species, including 14 introduced forms. Of these, 37 are referred to the Black Hills.

More recently (1926–1928) MCINTOSH (**14–17**) has investigated the flora of the Hills. The collection in the herbarium of the State

School of Mines at Rapid City, containing over 800 species of vascular plants, is largely the result of his personal work, and is the most extensive collection of plants of this region in existence. His first paper deals with the flora of Custer State Park. He lists the outstanding plants found in seven typical habitats: the foothills, the foothills streams, the mountains, the moist ravines, the valleys, the gorge, and the granite peaks. Among the 200 species of vascular plants listed are certain ones that are rare or peculiar to that part of the Hills, such as *Onoclea struthiopteris*, *Pinus flexilis*, *Viola blanda*, and *Myosotis alpestris*.

In a second paper he considers the sources of the flora of the Black Hills. On the basis of the distribution of 600 species, he finds that 6 per cent are common to the Northern Hemisphere, 16 per cent occur across North America, 7 per cent are of eastern origin, 17 per cent have come from the Great Plains, 36 per cent are of western origin, 6 per cent are from the north, 2 per cent have southern affinities, and 9 per cent are Old World weeds or escapes from cultivation.

A third paper deals with the Cascade Valley and vicinity, south of Hot Springs. In it he discusses the streamside vegetation, the inner valley, the main valley, the grassland, and sageland, noting the outstanding plants in each habitat.

PART I. FLORISTICS

During the summers of 1926 and 1927, collections were made at approximately fifty stations in the Black Hills and adjacent areas (fig. 1). The stations were selected in such a way that both geographical and formational distributions of the habitats were secured, as it was felt that the studies would then be representative of the region, and that a true picture of the floristic and successional relationships could be developed. The habitats were divided into four groups, representing (1) the prairie grassland type, (2) the conifer or montane forest, (3) the foothills chaparral, and (4) the upland meadow. In the first group were seventeen widely distributed stations which completely encircled the Hills; the second included fourteen stations located throughout the central region; in the third were eight lower canyon and foothills habitats, dominated by oak and

other deciduous trees and shrubs; and the fourth contained five upland meadows located for the most part in the Limestone District. In addition to these, special studies were made of the vegetation of the three principal peaks, and of the streamside and lakeside flora.

The collection,[3] which includes 765 species representing 341 genera and 91 families, doubtless contains the characteristic elements of the flora of the Black Hills, and an analysis of it should present an accurate representation of the floristic situation. It is in no sense complete, however, and probably includes only about one-half of the fernworts and seed plants of the region. A careful cross-check of the published lists of GRAY (**10**), RYDBERG (**22**), SAUNDERS (**24**), VISHER (**27–29**), and MCINTOSH (**14–17**) with that of the writer gives a total of nearly 1200 plants. A complete catalogue of the region would undoubtedly exceed this figure, as there are some collections that have not been reported as yet,[4] and further additions to the known flora may be expected as the territory is more completely studied.

COMPOSITION OF FLORA

The dominant flora of the Black Hills proper includes relatively few tree forms, belonging to nine families. First in importance is the Pinaceae, represented by *Pinus scopulorum*, *P. murrayana*, *P. flexilis*, and *Picea albertiana*. The yellow pine is the outstanding tree of the hills, with the northern spruce occurring frequently at the higher elevations and in the northern valleys. The lodgepole pine is restricted to one point in the hills, near Nahant, although there are a few widely scattered single specimens reported for other locations; and the limber pine occurs only in the Needles region near Harney Peak, on the Custer-Pennington county line. It is to these conifers that the Black Hills owe their name, for the approaching traveler sees them at a distance rising from the prairie as a blue-black mass.

The Fagaceae, represented by *Quercus macrocarpa*, dominate the

[3] A complete collection of the specimens obtained in the Black Hills has been deposited in the herbarium of the Public Museum, Milwaukee, Wisconsin, and will be preserved as a Black Hills unit.

[4] OVER is working on a revised flora of South Dakota which he expects to publish at an early date. Since this paper was written, MCINTOSH (**17**) has published a list of additions to the flora containing the names of 240 species.

lower valleys on the eastern slopes; with it are commonly found members of the Ulmaceae, *Ulmus americana* and *Celtis occidentalis*, the latter being more frequent in the southern valleys. Other tree families represented in the region are the Oleaceae by *Fraxinus pennsylvanica;* the Aceraceae by *Acer negundo;* Pomaceae by *Amelanchier alnifolia, Crataegus sheridana,* and *Sorbus scopulina;* and the Drupaceae by *Prunus melanocarpa, P. virginiana, P. americana, P. pennsylvanica,* and the shrubby *P. besseyi.* The Salicaceae are well represented along the streams by several species of willows and poplars, and the Betulaceae by *Betula fontinalis* and *B. papyrifera,* the latter occurring commonly in the secondary succession.

Shrubs occupy an important place in the open woodlands, and are the dominant forms in the chaparral of the foothills. Rosaceous forms are numerous, the following species being especially prominent: *Cercocarpus parvifolius, Rosa arkansana, R. woodsii, Dasiophora fruticosa, Physocarpus intermedius, Spiraea lucida, Rubus strigosus,* and *R. americanus. Rhus trilobata, R. rydbergii, Symphoricarpos occidentalis, S. racemosus, Shepherdia canadensis,* and *S. argentea* are very common in the drier situations; while *Sambucus racemosa, Viburnum pauciflorum, Cornus stolonifera,* and several species of *Ribes* are found in the more mesophytic habitats. *Ceanothus velutinus* occurs at the higher elevations, especially in the Limestone District.

Numerically, eight of the ninety-one families found in the region include over half of the total number of species, distributed as follows: Compositae 124, Gramineae 85, Leguminosae 56, Cyperaceae 36, Rosaceae 31, Ranunculaceae 26, Cruciferae 25, and Scrophulariaceae 20. The Compositae and Leguminosae are associated chiefly with the grassland formation, and show decided plains and western affinities. The grasses dominate the foothills and meadows, and penetrate into the yellow pine savannah and the oak chaparral. The sedges are found mainly with the mesophytic grasses in the upland meadows, although there are a few of the more xerophytic species that occur regularly in the prairie habitats. The Rosaceae are nearly 50 per cent western, and constitute an important element in the chaparral and open forest. The Ranunculaceae and Scrophulariaceae show no outstanding affinities, and the Cruciferae owe their numeri-

cal rank to the presence of a large number of ruderal forms in the Hills.

Other families that deserve special mention are the Orchidaceae and Euphorbiaceae. Eleven species representative of the former are distinctly northern, and are found in the cooler situations in the northern hills. The representatives of the latter family are southern, more than half of them being typical species of the south and southwest.

Geographic relationships

The isolated position of the Black Hills suggests the question of the sources of the flora. The ranges of 750 plants were determined, and they were then grouped into the following classes: (1) cosmopolitan species, (2) species ranging across the Northern Hemisphere, (3) species ranging across North America, (4) species proper to the Great Plains, (5) western species, (6) eastern species, (7) northern species, (8) southern species, (9) endemic species, and (10) ruderal species and Old World forms escaped from cultivation. This classification was used by McIntosh (**15**) in his study, and has been followed in order to make the results comparative.

Slightly in excess of 26 per cent of the species are characteristic of the Great Plains. This is what might be expected, as the plains completely surround the Hills, making contacts with the foothill chaparral and savannah associations; and, in many instances, penetrate the central regions and form prairie areas in the heart of the forest.

Species that are characteristically western comprise 25 per cent of the total. These may be divided into two groups: (1) those found with the western yellow pine and typical of the Rocky Mountains, and (2) those species that have migrated into the Hills from the western plains and foothills. In the first group are *Berberis aquifolium*, *Castilleja sulphurea*, *Frasera speciosa*, *Thalictrum venulosum*, *Lilium montanum*, *Geranium richardsonii*, *Vaccinium scoparium*, *Clematis pseudoalpina tenuiloba*, *Arnica cordifolia*, and *Ribes inerme;* the second category includes *Aristida fendleriana*, *Koeleria cristata*, *Sitanion hystrix*, *Carex filifolia*, *Artemisia tridentata*, *Lappula floribunda*, *Gaillardia aristata*, *Calochortus nuttallii*, *Rhus trilobata*, and *Cercocarpus parvifolius*.

Approximately 9 per cent of the species are typically eastern. They are usually found associated with *Quercus macrocarpa*, and include the following representative forms: *Ulmus americana*, *Acer negundo*, *Prunus virginiana*, *Celtis occidentalis*, *Aquilegia canadensis*, *Viola pubescens*, *Sanguinaria canadensis*, *Actaea rubra*, *Fragaria americana*, and *Unifolium* (*Maianthemum*) *canadense*.

Species that are characteristic of the north constitute about 6 per cent of the flora. In the yellow pine and spruce associations of the northern hills are found *Betula papyrifera*, *Viburnum pauciflorum*, *Linnaea americana*, *Gentiana plebeja*, *Circaea alpina*, *Calypso bulbosa*, *Limnorchis borealis*, *Moneses uniflora*, and *Corallorrhiza trifida*. In the upland meadows of the Limestone District are *Carex tenera*, *C. aenea*, *Torresia odorata*, *Calamagrostis canadensis*, *Juncus ensifolius*, and *Astragalus alpinus*.

Southern species that occur in the Hills comprise 5 per cent of the total. They are associated with the grassland and scrub formations, and for the most part are herbaceous forms that have migrated northward across the plains from the southwest. In this group are *Artemisia filifolia*, *Ipomoea leptophylla*, *Croton texensis*, *Euphorbia arkansana*, *E. dentata*, *Salvia lanceolata*, *Allionia linearis*, *Gaura parviflora*, *G. coccinea*, *Argemone intermedia*, *Aristida longiseta*, *Polygala alba*, and *Verbena bipinnatifida*.

As in most regions, a large number of the plants represent species of wide distribution. This group includes about 22 per cent of the flora, and may be subdivided further into three classes: (1) species that range across North America, comprising 17 per cent of the total flora; (2) species that extend across the Northern Hemisphere, 4.5 per cent; and (3) a few species that are truly cosmopolitan in character, 0.5 per cent. In the first class are such representative forms as *Populus tremuloides*, *Sambucus racemosa*, *Symphoricarpos racemosus*, *Cornus canadensis*, *Chamaenerion angustifolium*, *Anemone cylindrica*, *Salix fluviatilis*, *Viola adunca*, several species of *Carex*, *Pyrola*, *Equisetum*, and many grasses. In the second class are *Sagina saginoides*, *Eleocharis glaucescens*, *Triglochin palustris*, *Potamogeton pectinatus*, *Juniperus communis*, *Galium boreale*, *Limosella aquatica*, and several fernworts. Cosmopolitans occurring in the region in-

clude *Botrychium virginianum*, *Filix fragilis*, *Callitriche palustris*, and *Typha angustifolia*.

Ruderals are becoming increasingly common in the Black Hills, and comprise 6 per cent of the flora. These owe their presence in the territory primarily to the activity of man. Many are escapes from cultivation, others are ballast plants that have come in with the advent of the railroad, and a large number have been introduced with agricultural seeds. Without doubt several species have been able to invade the region because of superior devices for migration, a short vegetative cycle, and a structural organization that made ecesis possible. In this connection, it is of interest to note that 5 per cent of the additions to the flora reported in this paper are ruderal plants. This does not necessarily mean that these species have come into the region since the publication of previous lists. Some have doubtless done so, while others have become sufficiently widespread in their distribution to come into the hands of the collector.

The geographic grouping of the flora already indicated agrees essentially with the analysis made by McIntosh, except for the larger percentage of western species and a somewhat smaller proportion of southern ones reported in his paper. The fact that the present study included a number of outlying foothills habitats, dominated by species characteristic of the plains, would account for the larger percentage in that group and the relatively lower percentage of western forms.

The impression given by the preceding account of the floristic composition of the Black Hills would be extremely misleading without further analysis, based upon the local distribution of the plants in the various habitats studied. Since these will be discussed more completely later, four habitats representing wide divergences in floristic make-up will illustrate this detail of the situation.

The first habitat is known as Dark Canyon, located about 5 miles up Rapid Canyon from the Municipal Camp at Rapid City. It is a typical rocky canyon having precipitous sides abounding in crevice plants and topped by yellow pine. The floor of the canyon is occupied by oak, elm, boxelder, hackberry, several species of plums, and

various shrubs and herbaceous forms. Of 60 plants collected in this habitat, 30 per cent were eastern, 22 per cent North American, 18 per cent western, 12 per cent Great Plains, and 10 per cent northern.

FIG. 7.—Spearfish Canyon, showing northern spruce association

The remaining 8 per cent consisted of a few widespread forms and one species of *Aquilegia* that appears to be a new form.

Spearfish Canyon, from Savoy to a point approximately 4 miles above Cheyenne Crossing, is the second habitat. It is dominated by the yellow pine, with the northern spruce becoming more abundant upstream, and even assuming the dominant rôle on the north-facing

slopes (fig. 7). The habitat is cool and mesophytic, and the underflora is rich in northern and eastern species. A total of 126 plants was collected along this stream, with the following geographic distribution: northern forms 27 per cent, eastern 22 per cent, North American 22 per cent, western 20 per cent, Northern Hemisphere 5 per cent, Great Plains 1.5 per cent, and cosmopolitan 1.5 per cent.

Reynolds Prairie is representative of the grassland formation. Lying in the west-central portion of the Hills, and surrounded by towering limestone cliffs on the west and the yellow pine forest on

FIG. 8.—Reynolds Prairie: typical grassland association in the west-central hills; rim of Limestone Plateau seen in background.

the east, it presents a flora that is typical of the prairies and plains of the west (fig. 8). Of 50 species collected, 42 per cent were Great Plains types, 36 per cent western, 8 per cent North American, 6 per cent eastern, 4 per cent northern, and 4 per cent Northern Hemisphere.

The last illustration is drawn from a study made of the chaparral of the western foothills at a point near Newcastle, Wyoming (fig. 9). *Cercocarpus parvifolius* dominates, with other shrubs and herbs playing a minor rôle in the association. A total of 60 species was collected, of which 56 per cent were forms characteristic of the Great Plains, 25 per cent western, 10 per cent southern, 5 per cent North American, and 3 per cent northern; eastern species were entirely lacking.

Table I summarizes the results of the four studies. The contrasts are as striking as the figures indicate. In one habitat it would be easy to imagine one's self transplanted to a woodland dell in an eastern deciduous forest, another suggests the montane forest of the Rocky Mountains, and a third the open prairie. Thus, although there is no true floristic unity in the Hills, and although it is actually a meeting place of plants from all points of the compass, there still remains a

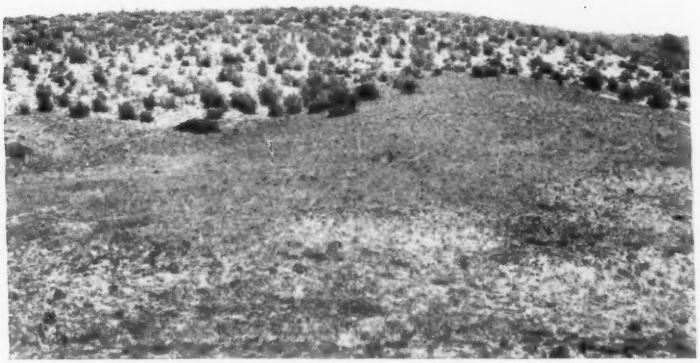

FIG. 9.—Chaparral formation near Newcastle, Wyoming, with *Cercocarpus parvifolius* dominating; zonation between chaparral and grassland very clearly defined at this point.

semblance of formational unity when the analysis is carried out on that basis. It is not a hopeless jumble, as one might conclude from the general analysis of the flora, but rather a vivid illustration of the fact that plants persist in habitats that are within the physiological limits of their range of adjustment, regardless of geographic affinities. The mesophytes from north, east, and west meet in the pine-spruce forest, and the xerophytes of the south mingle with those of the west and east on the foothills and prairies.

DISJUNCT SPECIES

In line with the general complexity of the flora is the occurrence of a large number of disjunct species. It would not be inaccurate to

consider all the tree forms as such, inasmuch as the Hills are completely encircled by grasslands; and it might further be argued with some justification that, by the same fact, all the plants of the Black Hills are disjuncts except those proper to the Great Plains. If the region is regarded as a great floristic island, isolated by climatic barriers and harboring elements from all points, then this conception is the correct one, and only those forms should be classed as continuous species that are now found in the intervening prairies and plains.

Thus the dominant yellow pine is disjunct from its main range in the Rocky Mountains; and other trees of more limited distribution, such as the bur oak, white spruce, lodgepole pine, limber pine,

TABLE I

Habitat	Dominant vegetation	No. of sp.	Geographic affinities, percentages							
			G.P.	W.	E.	N.	S.	N.A.	N.H.	Cos.
Dark Canyon.	Oak	60	12.0	18.0	30.0	10.0	0	22.0	3.0	3.0
Spearfish Creek.....	Pine-spruce	126	1.5	20.0	22.0	27.0	0	22.0	5.0	1.5
Reynolds Prairie.....	Grasses	50	42.0	36.0	6.0	4.0	0	8.0	4.0	0
Newcastle....	Cercocarpus	60	56.0	25.0	0	3.0	10.0	5.0	0	0

and others previously noted fall in the same category. The last two pines may be considered as local disjuncts as well as regional ones, since there are no special barriers to prevent extension of their ranges within the limits of the Hills; and the same term can be applied to many other species occurring in the region.

Among the herbaceous plants, one of the striking disjuncts is *Calypso bulbosa*. Two specimens of this dainty flower were found in the cool spruce forest along Spearfish Creek above Cheyenne Crossing. This is apparently the first time that this orchid has been found in the Hills. *Limnorchis borealis* grows in the same habitat, and *L. media* occurs in lower Spearfish Canyon. *Piperia unalaschensis* was found at two widely separated points, near Crooks Tower on the Limestone Plateau and on the hills above Pinecrest Park near Deadwood. *Viola bellidifolia* occurs in Dark Canyon, and *V. renifolia* was found only in upper Spearfish Canyon. The former is a western form, while the latter is distinctly northeastern.

Local disjunction is most strikingly illustrated in the case of the fernworts. Thus *Botrychium virginianum* is known to occur only in the vicinity of Deadwood near Pinecrest Park; *B. lanceolatum* in Spearfish Canyon above Savoy; and *B. neglectum*, according to RYDBERG, occurs south of Custer in the central hills. *Onoclea sensibilis* and *O. struthiopteris* are found on Squaw Creek just below the State Game Lodge, while *Adiantum modestum*[5] is indigenous along the banks of Cascade Creek south of Hot Springs.

The question which the occurrence of such a number of disjuncts raises is one of interpretation. What is the ecological significance of disjunction, and on what basis can it be explained? This problem can best be considered by grouping disjuncts into three classes: (1) habitat, (2) relict, and (3) pioneer or invader disjuncts.

In the first group are those forms that are disjunct solely because the habitat in which they can exist is itself discontinuous. In other words, the basis for disjunction is physiographic. This is well illustrated in the case of many of the more common hydrophytes that are found widely distributed in nature but are locally restricted to water holes, ponds, and lakes. Examples of this type of disjunct in the Black Hills are such forms as *Typha angustifolia*, occurring at Sylvan Lake; *Polygonum amphibium*, found in a water hole near Wind Cave; and *Marsilea vestita*, which occurs in water holes along the eastern foothills and in similar situations in the eastern part of the state.

Habitat disjunction may be edaphic rather than physiographic. This would occur where there are locally distributed areas that are strongly alkaline or acid in character. In the former the saline character of the habitat is the limiting factor, and acts to exclude all plants that lack salt tolerance. Examples of this type are not numerous, but the occurrence of an almost pure stand of *Distichlis spicata* in Hell Canyon is a good local illustration.

The relict disjuncts present quite a different situation. The group is interpreted as being a last outpost of a once more widespread distribution, which has survived in the face of changing conditions and the consequent shift in the character of the plant population.

[5] This fern was first reported by BESSEY as *A. capillus-veneris* L. BOT. GAZ. **26**: 211. 1898.

Discontinuity may be the result of changes in the intervening portions of the original range which did not affect the local habitat. In this case the relict may be able to resist competition successfully within the new limits established; but it will be unable to bridge the gap to its main range and reestablish continuity.

It is not easy to establish with certainty the past history of this type of disjunct, since the explanation involves a knowledge of prehistoric climatic changes that can only be determined on the basis of indirect evidence. In the case of the glacial relict there is the best opportunity for interpretation, since the limits of glaciation are fairly well defined, and the effect on the climate and vegetation can be rather accurately estimated. The northern white spruce is the best illustration of this type in the Black Hills, although many of the northern herbs, especially the bog orchids, doubtless owe their present isolation to the effect of glacial activity and subsequent climatic changes.

The pioneer or invader disjuncts represent the other extreme in plant dynamics. In general plant invasion is continuous and recession discontinuous, but this is not necessarily so. When the devices and agencies of plant migration are considered, it is not surprising to find new invaders that have successfully established themselves, and are at the same time entirely discontinuous from their main range. Prominent in this group are the ferns, and many of the ruderal and Old World forms that are becoming increasingly common in the Hills.

VEGETATIONAL HISTORY

It is not within the scope of this paper to inquire into the past vegetational history of the Black Hills, prior to the advent of the present flora,[6] but the presence of such a diversity of floristic elements in the Hills today raises the question as to their probable origins. Why are the eastern bur oak, the northern spruce, the western pines, and the various southern species in the region, and what was the sequence of their arrival?

[6] For a discussion of the fossil plants of the Black Hills, see WARD, L. F., Cretaceous formations in the Black Hills as indicated by fossil plants. U.S. Geog. Survey, 19th Ann. Rept. pt. II. pp. 521–946. 1899; also WIELAND, G. R., American fossil cycads. vol. II. Taxonomy. Carnegie Inst. Washington Publ. 34. p. 95. 1916.

COWLES (6), CLEMENTS (4), ADAMS (1), TRANSEAU (25), GLEASON (9), and many others have considered the problems of plant migration and succession, and as a result the essential principles of plant dynamics are generally understood. Much remains to be done in the field of prehistoric vegetational studies, however, and the complete story must await the fuller details which the paleobotanist and geologist may be expected to contribute, as research in these fields is continued. Until we have a more complete picture of past floras, especially of the more recent geologic periods, much of the story must be conjectural; but the body of evidence is sufficiently great to justify attempts to reconstruct the floristic record.

The significant feature of preglacial time, as it relates to present day floras, was the uplift of the Cordilleran Mountains which took place during Tertiary time. This had a profound effect upon the vegetational history of North America, as HARVEY (11) has pointed out. If the Cretaceous vegetation were somewhat uniform in its distribution, as is generally believed, the elevation of the Rocky Mountains, with the consequent aridity to the east, must be considered as the basic cause of vegetational segregation, which has resulted in the formation of the Great Plains and the north-south cleavage of the great forest centers of North America. According to GLEASON, the second cleavage was probably coincident with the approach of the first glacial period, and continued during the ice age. This led to the separation of the northern coniferous forests from the southern flora dominated by angiosperms.

Thus, during the glacial epoch, the climate of the Black Hills was undoubtedly favorable for the northern conifers, because of the southward extension of the invading ice sheet, and it was at that time that the northern spruce extended its range into the region. With the advent of milder and drier conditions, during the xerothermic period of Post-Wisconsin times, marked shifts in the distribution of the floral groups occurred. The coniferous belt moved northward and westward as the ice sheet receded, giving way to the prairie flora in the Great Plains and to the deciduous forests in the eastern United States. This movement resulted in the isolation of relict conifers in the more favorable habitats, such as the Black Hills. It seems

probable that during glacial time the spruce was the dominant tree in the Hills.

The invasion of the more xerophytic yellow pine, lodgepole pine, and limber pine from the west followed as the climate became drier and warmer. Finally the spruce continued to persist only at the higher elevations and in the colder valleys where conditions were favorable, and the yellow pine occupied the major portion of the central hills region.

Continued and probably increasing aridity favored further advances of the flora northward and eastward, resulting in the isolation of the Black Hills from the montane forest of the Rocky Mountains, and the invasion of the eastern deciduous forests. Some of the southern species may have established themselves in the Hills at this time, while others are the result of a more recent migration.

If postglacial climate had been uniform up to the present time, it would be difficult to account for the eastern elements in the region; but the investigations of BLYTT, ANDERSSON, SERNANDER, GEIKIE, and others, while not in agreement as to the details, indicate that there have been alternating periods of great climatic diversity since the last glacial epoch.[7] It is probable that there was a gradual change from the xerothermic conditions of early postglacial time to a more humid climate. This halted the invasion of the prairie into the forest, and swung the balance in the other direction. As a result there was an extension of the deciduous forest to the west and northwest along the river bottoms and adjacent highlands. The oak, elm, ash, boxelder, hackberry, and cottonwoods probably migrated up the Missouri and its tributary streams, and thus reached the Black Hills during the humid period.

The present isolation of these trees remains to be explained. The species found in the Hills also occur in the eastern part of the state, and many of them are distributed locally along the intervening streams; but there is little suggestion of continuity at the present time. Two explanations may be offered. The first is that the climatic cycle has swung around to another drier period, bringing with it

[7] For a summary of the work on postglacial climate, see CLEMENTS, F. E., Plant succession. Carnegie Inst. Washington Publ. 242. pp. 377–403. 1916.

conditions unfavorable for tree growth. This has favored an extension of the prairie grassland, and has restricted the tree forms to the more mesophytic locations in the river bottoms. The second possibility is that of human influence. If the tension line existing between the grassland and the forest were very finely drawn, any disturbance of this balance would react to the advantage of one over the other. Thus repeated burning of the prairie by the Indian, and deforestation by the pioneer, would tend to favor the gradual diminution of the deciduous forest. When the climate of the region west of the Missouri is taken into consideration, the first explanation appears to be the more satisfactory one; but humanistic factors were doubtless effective in hastening the process of isolation.

ENDEMISM

The question of endemism is always a difficult one. In a region that is definitely isolated, such as an oceanic island, the issue is obvious; but in the case of one that is a part of a continental area, it is always possible that the endemic plant may be in reality a disjunct of such infrequent occurrence that other stations have not been reported. Furthermore, the endemic may be only a variety of a more widespread species which appears temporarily in a habitat, due to unusual environmental conditions. It is desirable, therefore, that statements regarding new and endemic species should be extremely conservative and provisional. It seems likely that there are a few endemic species in the Black Hills, but definite confirmation must await the test of time. The following new species, which may possibly be endemic, have been determined tentatively by AVEN NELSON: *Aquilegia tenebrosa* A. Nels., *Lesquerella alpina argillosa* A. Nels., and *Solidago sigmoidea* A. Nels.

ADDITIONS TO FLORA AND EXTENSIONS OF KNOWN RANGES

The collections made in connection with these studies include a number of species that have not been reported in the previous lists of GRAY, RYDBERG, SAUNDERS, VISHER, BALL, and MCINTOSH. Where the addition also extends the known range of the species, the name is starred and the previous range indicated.[8]

[8] The ranges given are taken from RYDBERG, P. A., Flora of the Rocky Mountains and adjacent plains. New York. 1922.

Botrychium lanceolatum (Gmel.) Angstr., Spearfish Creek
Equisetum kansanum Schaffn., Hot Springs
Equisetum scirpoides Michx., Spearfish Canyon
Typha angustifolia L., Sylvan Lake
Lophotocarpus depauperatus (Engelm.) J. G. Sm., Water hole near Fairburn
Aristida longiseta robusta Merr., Hot Springs
Stipa columbiana Macoun.,* Deadwood (B.C.-Wyo.)
Calamagrostis purpurascens R.Br., Harney Peak
Aira caespitosa L., Inyankara Creek
Danthonia intermedia Vasey, Limestone District
Poa longipedunculata Scribn.,* Whitewood (Wyo.-N.M.-Utah)
" lucida Vasey, Common
" palustris L., Spearfish, Whitewood, Boxelder Creek
" trivialis L., Custer Peak and Deadwood
Bromus japonicus Thunb.,* Belle Fourche, Beulah, Hot Springs (Adv. from Eu.)
Agropyron dasystachyum (Hook.) Scribn., Reynolds Prairie
Agropyron riparium S. & S.,* Newcastle (Mont.-Colo.)
Hordeum pusillum Nutt., Buffalo Gap, Edgemont
Scirpus atrocinctus Fernald, Sylvan Lake
Carex abbreviata Prescott, Head of French Creek, Limestone District
" aenea Fernald, Limestone District
" bebbii Olney, Boulder Canyon, Boxelder Creek
" concinna R.Br.,* Spearfish Canyon (Rare in this range)
" eburnea Boott., Boulder Canyon, upper Spearfish Canyon
" hoodii Boott., Spearfish Canyon, Terry Peak, Limestone District
" obtusata Lilj., Boulder Park, Terry Peak
" rosea Schk., Rapid Creek and Dark Canyon
" rupestris All.,* Harney region (Rare alpine form)
" scoparia Schk., Sylvan Lake, French Creek
" xerantica Bailey, Limestone District
Tradescantia bracteata Small., Rapid City, Hermosa
Tradescantia laramiensis L. N. Goodding,* Hot Springs (Mont.-Col.-Utah)

Zygadenus intermedius Rydb.,* Common (Colo.-Wyo.)
Calypso bulbosa (L.) Oakes., Upper Spearfish Canyon (Very rare)
Limnorchis borealis (Cham.) Rydb., Spearfish Canyon (Rare)
Piperia unalaschensis (Spreng.) Rydb.,* Deadwood, Limestone District (Mont.-Colo.-Calif.-B.C.)
Corallorrhiza mertensiana Bong.,* Spearfish Canyon, Limestone District (Alaska-Mont.-Ida.-Calif.)
Populus candicans Michx., Rapid City
Ulmus fulva Michx., Hot Springs (Doubtful, identified without fruit)
Celtis crassifolia Lam., Hot Springs
Urtica viridis Rydb., Spearfish Canyon
Polygonum pratincola Greene., Needles Highway
Chenopodium paganum Reichenb., Ruderal (Adv. from Eu.)
Chenopodium subglabrum (Wats.) A. Nels., Edgemont
Amaranthus powellii S. Wats., Needles Highway
Montia parviflora depressa Robins, Whitewood Canyon
Lychnis alba Mill., Ruderal (Adv. from Eu.)
Stellaria crassifolia Ehrh., Upper Spearfish Canyon
Cerastium elongatum Pursh.,* Harney Peak (Mont.-No. Wyo.-Wash.)
Aquilegia tenebrosa A. Nels., n. sp., Dark Canyon
Batrachium flaccidum (Pers.) Rupr., Keystone
Thalictrum nelsonii Greene., Hot Springs, Inyankara and Boxelder Creeks
Arabis fendleri (Gray) Greene, Custer Peak
Erysimum tener A. Nels., Hot Springs (New species in ed.)
Lesquerella alpina argillosa A. Nels., Hermosa (New variety)
Draba nitida Greene, Boulder Park
Heuchera richardsonii R.Br., Common
Ribes hudsonianum Rich., Dark Canyon
Ribes irriguum Dougl.,* Dark Canyon, Boxelder Creek, Spearfish Canyon (B.C.-Mont.-Ida.-Ore.)
Potentilla ambigens Greene.,* Common (N.M.-Wyo.)
Potentilla paucijuga Rydb.,* Boulder Park (S.E. Utah)
Potentilla viridescens Rydb., Inyankara Creek
Amelanchier oreophila A. Nels., Limestone District

Astragalus elatiocarpus Sheld., Buffalo Gap
Oxytropis angustata (Rydb.) A. Nels., Hermosa, Fairburn, Buffalo Gap.
Amorpha fragrans Sweet., Hot Springs
Petalostemon mollis Rydb.,* Belle Fourche (Mont.-Colo.)
Meibomia canadensis (L.) Kuntze., Boulder Canyon
Vicia cracca L., Inyankara (Nat. from Europe)
Linum aristatum Engelm.,* Hot Springs (Greatly extends range)
Euphorbia arkansana Eng. & Gray., Belle Fourche, Wind Cave
Rhus osterhoutii Rydb.,* Hot Springs (Colo.)
Rhus oxyacanthoides (Greene) Rydb., Spearfish Creek
Rhamnus alnifolia L'Her., Bear Butte Creek
Ceanothus sanguineus Pursh.,* Spearfish Canyon (Mont.-No. Cal.-B.C.)
Viola renifolia Gray, Upper Spearfish Canyon
Epilobium saximontanum Haussk.,* Squaw Creek (Alta.-Wyo.-B.C.)
Oenothera muricata L., Spearfish Canyon, Harney Region, Hill City
Gaura glabra Lehm., Common on dry foothills
Pyrola minor L., Nahant and Harney region
Moneses uniflora (L.) Gray, Spearfish Canyon, Castle Creek
Androsace diffusa Small, Boulder Park, Wind Cave, Custer Peak
Convolvulus ambigens House, Beulah
Cryptantha crassisepala (T. & G.) Greene, Wind Cave
Mentha mollis L., Spearfish Canyon, Deadwood
Monarda ramaleyi A. Nels.,* Whitewood (Colo.)
Physalis subglabrata Mack., Hot Springs
Limosella aquatica L., Limestone District
Galium vaillantii DC., Hot Springs
Sambucus melanocarpa Gray, Boulder Canyon
Gutierrezia microcephala Gray,* Hot Springs (Colo.-Tex. and westward)
Grindelia erecta A. Nels., Newcastle
Chrysopsis bakeri Greene,* Sylvan Lake, Hot Springs (Wyo.-Ida.-N.M.-Utah)
Solidago sigmoidea A. Nels., n. sp., Limestone District
Solidago trinervata Greene, Belle Fourche, Spearfish, Sylvan Lake

Aster oblongifolius rigidulus Gray, Belle Fourche, Beulah, Hot Springs

Erigeron concinnus (H. & A.) T. & G., Beulah

" engelmannii A. Nels., Hot Springs

" laetevirens Rydb.,* Beulah, Buffalo Gap, Newcastle (Wyo.)

" montanensis Rydb.,* Common (Mont.-Wyo.)

" speciosus DC., Boxelder Creek

Antennaria howellii Greene,* Common (Alta.-Mont.-Ida.-Wash.-B.C.)

Antennaria marginata Greene,* Harney region (N.M.-So. Colo.-Utah.-Ariz.)

Antennaria oxyphylla Greene, Sylvan Lake

Helianthus giganteus L., Dry Gulch Rgr. Sta., Hot Springs

Helianthus subtuberosus Bourgeau, Needles Highway

Bidens prionophylla Greene, Hill City

Artemisia gnaphalodes diversifolia A. Nels., Belle Fourche

Artemisia purshiana Bessey, Deadwood, Hot Springs

Arnica rydbergii dubia A. Nels., Dark Canyon, Deadwood

Senecio fendleri Gray,* Rapid City, Hermosa, Boulder Park (N.M.-Colo.-Utah)

Senecio fendleri mutabile Greene, Beulah, Harney region, Limestone District

Tragopogon porrifolius L., Escape from cultivation

Hieracium scabriusculum Schwein., Boxelder Creek

Lactuca virosa L., Belle Fourche, Hot Springs (Nat. or adv. from Eu.)

Agoseris purpurea (Gray) Greene, Terry Peak, Rare (Colo.-N.M.-Ariz.-Utah)

PART II. SUCCESSIONAL STUDIES

The successional relationships in the Black Hills are intricate, as might be expected in a region having the floristic complexity indicated in the preceding section of this paper. It is desirable, therefore, to correlate the isolated units of vegetation in the region with the major formations of the western United States. Three major climaxes are generally recognized: (1) the grassland, (2) the scrub, and (3) the forest climax. Each is dominated by the life form

indicated, and is further subdivided into primary units, the formations, which in turn include one or more associations.

The formation is a climatic and physiographic unit which is characterized by one life form, namely, herb, shrub, or tree; but there need not necessarily be floristic unity. The association differs from the formation in this respect, and is here understood to be a subdivision of the latter having floristic unity. It is characterized by one or more dominant species, with which are associated numerous subdominants. These constitute the societies, and may be locally abundant, completely dominating limited areas within the association. The society is not an integral part of the association, however, but may occur in several associations within a formation. Further, the society commonly varies from the life form of the dominant species of the association. Thus there may be shrub societies in a grassland association, and herbaceous societies in the montane forest.

If the dynamic progress of vegetational development consists of a series of stages culminating in the formation, it is probable that a given region will contain units of vegetation that represent beginning and intermediate stages in such a succession. It is necessary, therefore, to include in a successional analysis a statement regarding the preclimax stages found, and to relate them to the climaxes toward which they are apparently developing.

In addition to the climax and preclimax stages, two others occur in the Black Hills. The first is the subclimax stage. This is preclimax in the succession; but it is sufficiently permanent to warrant special classification, since in many cases it has many of the characteristics of a climax situation. The second is the postclimax stage. This is represented by certain relict dominants, and is particularly significant because it indicates something of the past climaxes of the region.

Method of treatment

In arranging a scheme of classification on the basis of the preceding, it has seemed advisable to group together the climax, postclimax, and subclimax stages under the three major formations, even though the last two are not strictly climax units; and to consider

separately the preclimax or developmental stages. This treatment permits a discussion of the principal vegetational units in the order of their occurrence, from the prairie to the central hills; and, in consequence, should give a more understandable picture of the sequence of associations and the contacts existing between them.

Synopsis of successional relationships

I. Climax and late successional stages
  1. Grassland climax
    a. Mixed prairie association
  2. Scrub climaxes
    a. Sagebrush subclimax; Artemisia association
    b. Petran chaparral climax; Cercocarpus-Rhus association
    c. Chaparral subclimax; Quercus-Rhus association
  3. Forest climaxes
    a. Deciduous forest postclimax; Quercus association
    b. Petran montane forest climax; Pinus scopulorum association
    c. Boreal forest postclimax; Picea albertiana association
    d. Secondary succession subclimax
      1. Pinus murrayana association
      2. Betula-Populus association

II. Preclimax or developmental stages
  1. Hydric series
    a. Pond stage
    b. Streamside stage; Betula-Salix association
    c. Upland meadow stage; Grass-sedge association
  2. Xeric series
    a. Rock pioneer stage
    b. Erosion pioneer stage
    c. Secondary succession pioneer stage

I. Climax and late successional stages

Grassland climax

Mixed prairie association.—The grassland climax is represented in the Black Hills and adjacent plains by the mixed prairie association. Studies of this type were made at Sturgis, Rapid City,

Hermosa, Fairburn, Buffalo Gap, Hot Springs, Edgemont, Hell Canyon, Inyankara, Beulah, Belle Fourche, Wind Cave, Reynolds Prairie, and Boulder Park. The last two are in the Hills proper; the others are habitats where the prairie extends up to and makes contact with the chaparral, deciduous forest, or yellow pine on the foothills (fig. 10). Available data for nine of these stations give an

FIG. 10.—Contact zone between yellow pine and mixed prairie in northern foothills; the yellow pine extends down rocky ridges.

average annual rainfall of 17.56 inches, the precipitation being greater on the eastern foothills than on the western, where it falls below 16 inches.

As the name suggests, the mixed prairie represents a grassland association in which the tall grasses of the true prairie and the short bunch grasses of the plains intermix and maintain equilibrium, the latter occurring as an understory of the former. Thus, in the habitats studied, the prairie dominants *Koeleria cristata*, *Stipa comata*, *Agropyron smithii*, and *A. spicatum* occur as codominants with the short grasses and sedges *Bulbilis dactyloides*, *Bouteloua gracilis*, *Carex stenophylla*, and *C. filifolia*. *Koeleria cristata* is the most abundant of the prairie grasses, occurring in thirteen of the fourteen habitats

studied. *Stipa comata* is one of the common dominants, and *S. viridula* is occasionally found with it. *Agropyron* is much less common than either of the two preceding genera. *Bulbilis dactyloides* is the most abundant of the short grasses, with *Bouteloua gracilis* second in importance. At least one of the two species of *Carex* occurs at ten of the stations. The most common groupings of the dominants are: *Koeleria-Stipa-Bulbilis; Koeleria-Stipa-Agropyron-Bouteloua-Carex; Stipa-Bouteloua-Carex; Koeleria-Bouteloua-Bulbilis;* and *Koeleria-Bouteloua.*

In addition to the dominant grasses, several others occur frequently. *Calamovilfa longifolia, Andropogon furcatus,* and *A. scoparius* represent the true prairie, while *Aristida longiseta, A. fendleriana, Sitanion hystrix,* and *Distichlis spicata* suggest the short grass plains of the west and southwest.

With the grasses in the association are numerous societies of perennial herbs. The great majority of these are identical with the societies found in the true prairie; others are characteristic of the plains; while a few have invaded the grassland from the chaparral. They constitute an important element in the mixed prairie, and due to them the seasonal aspects of the association show striking variations.

Societies

Vernal aspect:

Carex brevior
Leucocrinum montanum
Calochortus nuttallii
Sisyrinchium angustifolium
Erysimum asperrimum
Erysimum asperum
Sieversia ciliata
Prunus besseyi
Astragalus caespitosus
Astragalus crassicarpus
Astragalus gracilis
Oxytropis saximontana
Euphorbia montana
Musineon tenuifolium
Oreocarya glomerata
Mertensia lanceolata
Lithospermum angustifolium
Onosmodium occidentalis
Pentstemon albidus
Castilleja sessilifolia
Antennaria aprica
Achillea lanulosa

Estival aspect:

Allium reticulatum
Yucca glauca
Zygadenus intermedius
Comandra pallida
Eriogonum crassifolium
Eriogonum multiceps
Paronychia sessilifolia
Drymocallis arguta
Astragalus nitidus
Oxytropis dispar
Psoralea argophylla
Psoralea esculenta
Psoralea tenuiflora
Petalostemon oligophyllus
Petalostemon purpureus
Linum rigidum
Polygala alba
Malvastrum coccineum
Opuntia polyacantha
Meriolix serrulata
Gaura glabra
Lappula occidentalis
Pentstemon gracilis
Orthocarpus luteus
Campanula rotundifolia
Antennaria obovata
Brauneria angustifolia
Hymenopappus filifolius
Actinella simplex
Senecio canus purshianus
Senecio fendleri
Lygodesmia juncea

Serotinal aspect:

Liatris punctata
Gutierrezia sarothrae
Chrysopsis foliosa
Solidago missouriensis
Solidago pulcherrima
Aster ptarmicoides
Artemisia frigida
Artemisia gnaphalodes
Cirsium megacephalum

The permanence of the mixed prairie depends upon the ability of the tall grasses to maintain themselves successfully. They are apparently able to do this in areas that are not subject to severe grazing; but in other areas, notably along the southern foothills where there has been considerable grazing, the prairie grasses are less abundant, and there is a marked increase in such species as *Artemisia frigida* and *Opuntia polyacantha*. At one point south of Hot Springs there is an overgrazed area which is completely dominated by cactus and sage.

Where the rainfall does not exceed 18 inches, the grassland is able to persist along the tension line with the chaparral, and may

even invade the scrub and the pine savannah to some degree; but where the precipitation exceeds this figure, the grassland gives way to the deciduous forest and the yellow pine. A very slight change in the direction of more moist conditions would result in the extension of the forest area beyond its present limits, while a swing in the other direction would materially reduce the forested zone and permit further extension of the grassland into the Hills.

Scrub climaxes

Sagebrush subclimax; Artemisia association.—The sagebrush association may be regarded as an eastern extension of the

Fig. 11.—Sagebrush association south of Cheyenne River; cultivated fields on right suggest indicator value of sage; secondary succession ruderals seen along roadway.

Basin sagebrush, which makes contact with the mixed prairie along the southern and western foothills, being especially well defined in the former location. The habitat selected as representative of this type is located about 20 miles southwest of Hot Springs, on the lower Edgemont road. After crossing the Cheyenne River the sage occurs much more abundantly, and closely resembles the situation found in the Great Basin (fig. 11).

The dominant species is *Artemisia tridentata*, with *A. filifolia* and *A. cana* as codominants. Other sages in the association are *Artemisia*

frigida, *A. gnaphalodes*, *A. caudata*, and *A. canadensis;* but these do not hold an important place in the plant groupings, and are commonly found in the mixed prairie. *Chrysothamnus graveolens*, *Gutierrezia sarothrae*, and *Sarcobatus vermiculatus* are the principal subdominants, the last being abundant in the more saline situations.

The subclimax character of this association is indicated by the presence of many grasses and societies of the mixed prairie, which tend to supersede the sage, except under conditions of overgrazing, as a result of successful competition for water. Where the rainfall is below 16 inches annually the sage assumes a permanent character, which would justify classification of the association as climax rather than subclimax; but the majority of cases indicate that it is subclimax to the mixed prairie.

Grasses of mixed prairie in sagebrush subclimax

Agropyron smithii	Bulbilis dactyloides
Bouteloua gracilis	Sitanion hystrix

Societies

Tradescantia laramiensis	Opuntia fragilis
Erysimum asperrimum	Gaura glabra
Psoralea tenuiflora	Pentstemon albidus
Petalostemon purpureus	Liatris punctata
Linum rigidum	Lygodesmia juncea

PETRAN CHAPARRAL CLIMAX; CERCOCARPUS-RHUS ASSOCIATION.—The chaparral occupies an intermediate zone between the mixed prairie and the montane forest, and is represented in the Black Hills by the *Cercocarpus-Rhus* association. Constituting an extension of the Rocky Mountain chaparral, it occurs chiefly on the western slopes, where it represents the eastern limit of the association. The chaparral is not a continuous zone, being much interrupted by the irregularities of the topography of the region. In places where it is lacking, the grassland makes direct contact with the yellow pine forest.

A good example of this association is located on the South Dakota–Wyoming state line near the L.A.K. ranch, and about 12

miles southeast of Newcastle on Highway 36. At this point there is a typical chaparral dominated by *Cercocarpus parvifolius* and *Rhus trilobata*, with the former occurring in almost pure stands at several stations (fig. 9). *Symphoricarpos racemosus* and *Rosa arkansana* are present, but do not occur as frequently as in the subclimax chaparral of the eastern foothills.

The association is of the open savannah type, and includes many grasses and societies of the mixed prairie as well as societies that are characteristic of the forest. Since the majority of the species are drawn from the climax associations in contact with it, it cannot be considered as having an underflora peculiar to itself. In the open spaces are societies of the prairies, and in the protecting shade of the shrubs are found the forest elements.

Grasses of mixed prairie

Agropyron riparium
Aristida fendleriana
Bouteloua curtipendula
Bouteloua gracilis
Koeleria cristata
Oryzopsis hymenoides
Sitanion hystrix
Stipa comata

Societies

Woodsia oregana
Juniperus scopulorum
Allium reticulatum
Calochortus nuttallii
Zygadenus intermedius
Paronychia sessilifolia
Pulsatilla patens
Argemone intermedia
Erysimum asperrimum
Heuchera richardsonii
Oxytropis saximontana
Psoralea esculenta
Petalostemon purpureus
Polygala alba
Euphorbia fendleri
Malvastrum coccineum
Gaura coccinea
Musineon tenuifolium
Oreocarya glomerata
Hedeoma hispida
Castilleja sessiliflora
Campanula rotundifolia
Chrysopsis foliosa
Brauneria angustifolia
Hymenopappus filifolius
Actinella simplex
Achillea lanulosa
Artemisia frigida
Cirsium megacephalum

The fact that the societies of this association are in reality invaders from the associations in contact with it, raises the question as

to whether or not it is correct to consider the chaparral as a climax type. Is it not similar in this respect to the sagebrush subclimax? The difference lies in the fact that the sagebrush is actually replaced by the grasses in the succession, while the invader societies in the *Cercocarpus-Rhus* association merely occupy the open spaces between the shrubs, and do not appear to compete successfully with them once they are established. Further, it should be noted that at certain points *Cercocarpus* occurs as a pure stand without any of the underflora previously listed. In view of these facts, and considering that it is clearly a climax type farther west, it seems desirable to classify the Petran chaparral as a relict outpost of a true climax type, which will hold its position in an intermediate climatic zone where the rainfall is approximately 16 inches annually.

CHAPARRAL SUBCLIMAX; QUERCUS-RHUS ASSOCIATION.—The subclimax chaparral occurs as an intermediate zone along the eastern foothills, between the mixed prairie and the montane forest, and also extends eastward along the stream valleys. It occupies the same relative position on the eastern foothills that the *Cercocarpus-Rhus* association holds on the western, but is quite different in its affinities, being definitely related to the marginal type found along the deciduous forest of the east. Like the Petran chaparral, it is not a continuous belt, but occurs chiefly in the lower valleys of the eastern streams and in some instances extends well up into the hills (fig. 12). Studies of this type were made at Belle Fourche, lower Spearfish Canyon, Whitewood, Boulder Canyon, and Hot Springs.

The dominant vegetation is chiefly shrubby, but there are a few trees intermixed which are somewhat dwarfed because of the xerophytic conditions of the habitat.

Dominants

Corylus rostrata
Quercus macrocarpa
Rosa arkansana
Rosa woodsii
Amelanchier alnifolia
Crataegus sheridana
Prunus americana
Prunus besseyi
Prunus melanocarpa
Prunus virginiana
Rhus cismontana
Rhus trilobata
Shepherdia argentea
Cornus stolonifera
Symphoricarpos occidentalis
Symphoricarpos racemosus

In addition to the bur oak, hawthorn, and plums mentioned, there are several other trees that occasionally are associated with this group, although they properly belong to the deciduous forest. These are *Ulmus americana*, *Fraxinus pennsylvanica*, *Ostrya virginiana*, *Acer negundo*, and *Celtis occidentalis*. As in the case of the mountain chaparral, the societies are derived from the adjacent forest and grassland associations, although some of them reach their highest development in the scrub community. The twofold character of the important societies is indicated in the following lists.

Woodland or forest societies

Pteris aquilina
Filix fragilis
Disporum trachycarpum
Unifolium canadense
Smilacina sessilifolia
Urtica viridis
Aquilegia canadensis
Thalictrum venulosum
Sanguinaria canadensis
Vicia americana
Lathyrus ochroleucus
Geranium richardsonii
Rhus rydbergii
Viola adunca
Viola pubescens
Aralia nudicaulis
Sanicula marylandica
Washingtonia longistylis
Galium aparine
Galium boreale
Arnica cordifolia

Grassland societies

Zygadenus elegans
Anemone cylindrica
Erysimum asperum
Astragalus carolinianus
Psoralea esculenta
Verbena stricta
Monarda ramaleyi
Campanula rotundifolia
Solidago missouriensis
Rudbeckia hirta
Artemisia gnaphalodes
Tragopogon porrifolius

Grasses and sedges are not uncommon in this association, species characteristic of the mixed prairie being prominent in the more open phases of the chaparral. In the more mesophytic locations, where the shrubs grow taller and closer together, the meadow species *Phleum pratense*, *Poa palustris*, and *Agrostis palustris* occur.

The subclimax character of this association is suggested by its heterogeneous floristic composition and by the variability of its

aspects. Unlike the *Cercocarpus-Rhus* association, it has no single dominant or group of dominants, varying widely in this respect in the different habitats observed. Further, it apparently lacks the stability of a climax association, and appears to be going over to grassland on the one side and coniferous forest on the other. It suggests a relict vegetation of a wetter climatic cycle which is gradually losing ground under present conditions.

FIG. 12.—Stand of *Quercus macrocarpa* at mouth of Boulder Canyon near Sturgis, representing intermediate zone between grassland and montane forest.

FOREST CLIMAXES

DECIDUOUS FOREST POSTCLIMAX; QUERCUS ASSOCIATION.—The deciduous forest is very poorly represented in the Black Hills, and is undoubtedly a remnant of a once more extensive oak-hickory association of which but a few dominants remain. The probable history of this association has already been discussed, but the successional relationships require a brief statement.

The trees that make up this association are the same as occur as dwarf forms in the subclimax chaparral; and there would be no justification for including this association in the present analysis were it not for the fact that, at a few points, they attain treelike dimensions. In several places, notably at Whitewood, Dark Canyon, and Spearfish, the oak becomes a rather large tree of forest propor-

tions, and it would be inaccurate to classify it and the associated trees as subclimax chaparral. *Quercus macrocarpa* is the sole dominant; but with it are several other trees of subdominant rank, *Ulmus americana*, *Fraxinus pennsylvanica*, *Acer negundo*, and *Celtis occidentalis*.

The societies are not essentially different from those noted for the subclimax chaparral, except for the greater number of mesophytic herbs and fewer species characteristic of the grassland. In fact there is no sharp line of demarcation between the oak chaparral and the oak forest, the latter being merely the response of the same species to more favorable conditions. For this reason, the oak association is considered as postclimax, since it is an expression in terms of limited growth and development of what was once a much more widespread condition. Locally in the more favorable habitats, the association is undoubtedly climax rather than postclimax, as it is maintaining itself successfully and even slightly extending its range. In general, however, it is a relict type which is passing back through the chaparral stage to the grassland on the one hand, and being replaced by the more xerophytic yellow pine on the other.

PETRAN MONTANE FOREST CLIMAX; PINUS SCOPULORUM ASSOCIATION.—The montane forest is the outstanding association in the Black Hills, dominating the central areas and extending projecting arms down the rocky ridges of the foothills, where it makes contact with the chaparral and the mixed prairie (fig. 10). The forested region lies mainly within the limits of the Harney and Black Hills National Forests and Custer State Park, which have a combined area of approximately 1,435,000 acres. In addition to this there is a considerable acreage that is privately controlled by mining companies and other interests. Not all of this area is timbered, however, as one of the striking features of the forest is the occurrence of numerous open parks, meadows, and prairies, which in some instances are very extensive.

This eastern outlier of the great coniferous forests of the Rocky Mountains is dominated by *Pinus scopulorum*, which grows in almost pure stands, differing in this respect from the yellow pine forests of the West, where it often is associated as a dominant with *Pseudotsuga mucronata*, *Abies concolor*, and *Pinus murrayana* (5).

Picea albertiana occurs as a subdominant in the Harney region and on the more moist slopes in the northern valleys; *Pinus murrayana* occurs in but one locality, forming a subclimax association in the vicinity of Nahant; and there is a small society of *Pinus flexilis*, numbering about forty mature trees, in the Needles on the boundary line between Pennington and Custer counties.

Pinus scopulorum is the most xerophytic of the dominants of the montane forest, which doubtless accounts for its extension beyond the range of the other members of this formation. In Arizona and New Mexico, WOOLSEY (**32**) finds that "no stand of large extent is likely where the annual rainfall is less than 20 inches." Scattering stands do occur in that region on northerly exposures with as little as 16.6 inches. This agrees essentially with the situation in the Black Hills, where the best stands of yellow pine are found in the central and northern regions, in which the average annual rainfall ranges from 21.34 to 24.45 inches. In the drier habitats at Hot Springs and Belle Fourche, where the rainfall is 18.41 and 15.03 respectively, the yellow pine grows as an open savannah and fails to develop good mature stands.

The savannah represents the first of three rather well defined aspects of the yellow pine association, and occurs near the contact zones with the chaparral, where the rainfall is 15–18 inches. In this phase the trees are widely scattered in discontinuous clumps, and the intervening spaces are occupied by grassland of the mixed prairie type. There is little evidence of reproduction, and the pines are stunted and lacking in vigor.

The second aspect is the open park. This is the most common type in the Hills, and occurs in situations where the rainfall is 20–22 inches. Here the pines grow to full maturity, attaining a height of 75 feet or more, reproduction is adequate, and the light factor is favorable for sapling development. With the yellow pine in this phase, there is usually a scattering of *Picea albertiana*, *Populus tremuloides*, and *Betula papyrifera*, the last two being related to a secondary stage in the succession.

In addition to these there is an understory of shrubs, which are in part species characteristic of the chaparral and the deciduous forest associations.

Shrub societies

Juniperus sibirica
Corylus rostrata
Ostrya virginiana
Berberis aquifolium
Ribes cereum
Ribes inerme
Ribes setosum
Physocarpus intermedius
Spiraea lucida
Rubus americanus
Rubus strigosus
Rosa arkansana
Amelanchier alnifolia
Ceanothus sanguineus
Cornus stolonifera
Arctostaphylos uva-ursi
Sambucus racemosa
Viburnum pauciflorum
Symphoricarpos racemosus
Lonicera glaucescens

The third aspect is the closed forest. This is more mesophytic than either of the preceding, with a rainfall approximating 24 inches. It is found in the northern hills, but the number of mature stands is limited because of the extensive use of the pine for mining purposes, severe losses by fire, and *Dendroctonus* beetles. The second growth stands are developing into this closed type, and density of stand rather than reproduction is one of the practical problems confronting the forester.

Shrubs are less abundant in the closed type, and are replaced by numerous herbaceous societies. There is no sharp line separating the open park from the closed forest, so that the societies listed are in general characteristic of both phases. The seasonal aspects are best expressed by grouping into two rather than three divisions, as the serotinal aspect is not clearly differentiated. It should be noted that many of the spring-blooming species continue on well into the summer.

Herbaceous societies

Vernal aspect:

Filix fragilis
Woodsia oregana
Oryzopsis asperifolia
Unifolium canadense
Disporum trachycarpum
Clematis pseudoalpina tenuiloba
Actaea rubra
Thermopsis rhombifolia
Vicia americana
Lathyrus ochroleucus
Polygala senega
Viola adunca
Viola canadensis
Aralia nudicaulis

Cornus canadensis
Mertensia lanceolata
Galium boreale
Valeriana ceratophylla
Antennaria howellii
Antennaria parvifolia

Estival aspect:

Lilium montanum
Smilacina sessilifolia
Limnorchis hyperborea
Peramium repens
Corallorrhiza multiflora
Thalictrum venulosum
Aconitum ramosum
Geranium richardsonii
Epilobium adenocaulon
Sanicula marylandica
Zizia cordata
Pyrola minor
Pyrola secunda
Pterospora andromeda
Frasera speciosa
Castilleja sulphurea
Linnaea americana
Valeriana occidentalis
Aster laevis
Aster lindleyanus
Aster ptarmicoides
Erigeron glabellus
Anaphalis subalpina
Arnica rydbergii
Senecio canus purshianus
Senecio flavulus

The relation between forest and grassland, where they make contact along the margins of the meadows and prairies, is difficult to interpret. Apparently the two formations are in equilibrium, as there is no evidence that either is extending its range at the present time. The occurrence of parks and prairies, within the main limits of the yellow pine association, is a characteristic that has been observed wherever this association is found; and there are many examples of this throughout the Hills, especially at Reynolds Prairie and in the Limestone District.

The explanation of this situation is probably tied up with the influence of climatic and edaphic factors on yellow pine reproduction. PEARSON (**20**) has made extensive studies of the reproduction of the yellow pine in the southwest, and finds that "reproduction is better on the coarser, sandy, gravelly, or stony soils than on the finer soils regardless of geologic origin." The meadows and prairies have a soil of very fine texture, and the softness and depth of this surface material explain in part the absence of trees. It is possible that the absence of trees in the Red Valley is due to this same factor, as they occur on the Hogback Ridge outside of the valley where the climatic

conditions are the same. Once the tree has established itself, its soil requirements are not sharply delimited; but it does best on the limestone formations, where the largest trees and the finest stands are to be found.

The protection afforded the seedlings by the mature trees is an important factor. The effect of this cover is to reduce air movement, with a consequent decrease in transpiration, and to moderate the temperature, thus reducing the amount of winter killing in the seedling crop. On the other hand, the yellow pine is intolerant of shade except in the early seedling stage, and saplings coming up under mature stands will not reach maturity. The best reproduction is obtained in the open park, where a reasonable degree of cover protection is provided, with sufficient light to meet later growth requirements.

The fact that the pine grows on the Hogback Ridge, on the exposed ridges of the foothills, and on such outlying extrusions as Bear Butte suggests that the edaphic factor is the limiting one rather than the climatic factors, where the average annual rainfall exceeds 18 inches. Below that figure successful competition is impossible, and the forest is replaced by chaparral and grassland.

BOREAL FOREST POSTCLIMAX; PICEA ALBERTIANA ASSOCIATION.—Although the white spruce is commonly found in the yellow pine association, it does not properly belong to the climax montane forest, but should be considered as a straggler from the boreal forest. This is indicated by the fact that the spruce dominates only in the colder situations, where the factors of moisture, exposure, and temperature approximate those of its main range. This is well illustrated in upper Spearfish Canyon, where the spruce replaces the yellow pine (fig. 7). At Savoy the two trees occur in equal numbers, but beyond Cheyenne Crossing and upstream for several miles, the north-facing slopes are covered by a stand in which the spruce is the dominant tree.

This type of association is not widespread, but it is sufficiently definite, where it does occur, to warrant separate treatment. In view of the probable vegetational history of the spruce, it seems proper to regard the association as a postclimax relict of a once more widespread boreal forest. The societies found are practically identical with those of the yellow pine association, but there are a few additional species that should be noted.

Societies

Botrychium lanceolatum	Geranium viscosissimum
Carex peckii	Viola pubescens
Cypripedium parviflorum	Viola renifolia
Calypso bulbosa	Circaea alpina
Peramium repens	Moneses uniflora
Aquilegia brevistyla	Dodecatheon pauciflorum
Fragaria americana	Mimulus langsdorfii

SECONDARY SUCCESSION SUBCLIMAX; PINUS MURRAYANA ASSOCIATION.—The lodgepole pine is not abundant in the Black Hills, and occurs in sufficient numbers to constitute an association only in the vicinity of Nahant. Isolated specimens have been reported as occurring on the old road between Rapid City and Hill City, near the Hardy Ranger Station, and south of Custer Peak. The habitat studied lies just west of the Chicago, Burlington and Quincy tracks on the north fork of Rapid Creek, about three quarters of a mile south of the Bulldog Ranch.

The association is a typical secondary succession community, and closely resembles the lodgepole burn forests of Colorado described by CLEMENTS (3). It represents a subclimax stage to the yellow pine climax, which is gradually replacing it. At the present time there are areas where about 75 per cent of the trees are lodgepole pine, but in the major portion of the region the yellow pine is codominant with the lodgepole, and in some places has become the dominant tree. The secondary character of the association is indicated by the societies, which include many plants commonly found in the burn forest. Chief among these are *Populus tremuloides*, *Betula papyrifera*, *Vaccinium scoparium*, *Chamaenerion angustifolium*, *Sedum stenopetalum*, *Anaphalis subalpina*, *Rudbeckia hirta*, *Arctostaphylos uva-ursi*, and *Drymocallis arguta*.

SECONDARY SUCCESSION SUBCLIMAX; BETULA-POPULUS ASSOCIATION.—This association represents another aspect of the secondary succession which follows burning or clear cutting. Where the lodgepole is present, the birch-aspen association constitutes a preclimax stage leading up to the lodgepole subclimax; but, in the absence of the lodgepole, it becomes a subclimax stage which directly precedes the yellow pine climax (fig. 13).

A good example of this association is found on the slopes of Terry Peak, above the town of Trojan, where fire and mining operations have resulted in the destruction of the original stand of yellow pine. *Populus tremuloides* and *Betula papyrifera* are the dominant trees, with which are *Prunus melanocarpa*, *P. americana*, *P. pennsylvanica*, and *Sorbus scopulina*. The presence of young pines and

FIG. 13.—Secondary succession of birch and aspen near Cheyenne Crossing; scattering specimens of pine and spruce seen throughout association.

spruces indicates the direction of the succession toward the montane forest climax. The societies in this association, like the preceding one, include many species that are characteristic of the secondary succession.

Societies

Pteris aquilina
Juniperus sibirica
Oryzopsis asperifolia
Clematis pseudoalpina tenuiloba
Sedum stenopetalum
Rubus strigosus
Fragaria americana
Geranium richardsonii
Chamaenerion angustifolium
Aralia nudicaulis
Arctostaphylos uva-ursi
Vaccinium scoparium
Castilleja sulphurea

II. Preclimax or developmental stages

Hydric series

Pond stage.—Although the region is characteristically dry and inclines toward the xeric side in its climax stages, there are numerous small ponds and water holes that persist throughout the summer, except in seasons of extreme dryness. They have a characteristic hydric flora, including many cosmopolitan species which occur in several different groupings. Thus, in a pond between Fairburn

Fig. 14.—*Marsilea vestita* and *Eleocharis palustris* in a pond association between Fairburn and Buffalo Gap.

and Buffalo Gap, there is a *Marsilea vestita-Eleocharis palustris* combination, the former occupying the inner zone and the latter dominating the outer (fig. 14). With the latter are *Eleocharis acicularis*, *Lophotocarpus depauperatus*, and *Gratiola virginiana*. These are replaced by *Carex brevior* and various prairie grasses along the outer margin. In a pond near Hot Springs, the grouping is *Eleocharis glaucescens*, *Juncus torreyi*, and *Roripa nasturtium-aquaticum*. At Beulah, in a water hole and swale, the grouping is *Eleocharis glaucescens*, *Scirpus americanus*, *Juncus ater*, and *Carex praegracilis*. Other combinations include *Sagittaria arifolia-Herpestes rotundifolia* found south of Rapid City; *Eleocharis glaucescens-Polygonum amphibium-Heteranthera limosa* near Wind Cave; and *Typha latifolia* at Aztec.

Sylvan Lake in the Harney region is the only lake in the Hills. It is not a natural one, but has been formed by the construction of a dam at its west end, which impounds the headwaters of the south fork of Spring Creek. It is bounded by towering rocks on three sides, but its eastern margin is low and swampy. At this point there is a typical *Typha-Juncus-Scirpus* association. The cattail is the rarer *Typha angustifolia*, with which are *Juncus brevior*, *Scirpus atrocinctus*, *Carex rostrata*, *C. scoparia*, *Panicularia grandis*, *Ranunculus pennsylvanicus*, *Mentha glabrior*, and *Scutellaria galericulata*.

STREAMSIDE STAGE; BETULA-SALIX ASSOCIATION.—The numerous streams that arise in the Limestone District, flow outward to the Red Valley, and thence to the Cheyenne and Belle Fourche rivers, have a vegetation characterized by shrubby dominants that are principally members of two genera, *Salix* and *Betula*. *Populus* is well represented at the lower limits of the streams, but gradually disappears upstream.

Studies of the streamside were made at four points, Castle Creek above Deerfield and Boxelder Creek above Nemo, representing the upper phase of the association; and Spearfish Creek and Hot Brook Creek, illustrating the successional relationships at the lower limits.

The upper reaches of these mountain streams are characterized by a dense growth of shrubs that occupies the margin of the stream and completely screens it from view. The most common dominants are *Betula fontinalis*, *Salix bebbiana*, *S. scouleriana*, and *S. fendleriana*. Other shrubby forms which are found sparingly intermixed with the four dominants are *Salix fluviatilis*, *S. exigua*, *Cornus stolonifera*, *C. baileyi*, *Prunus melanocarpa*, *Corylus rostrata*, *Amelanchier alnifolia*, *A. oreophila*, *Rosa woodsii*, *Ribes inerme*, and *Rubus americanus*. The herbaceous flora consists of the hydrophytic societies that grow in the water or along the water's edge, and the mesophytic societies that grow on the banks under the shade of the dominant shrubs.

Hydrophytic societies

Equisetum arvense	Triglochin palustris
Equisetum laevigatum	Alopecurus aequalis
Potamogeton heterophyllus	Calamagrostis canadensis
Potamogeton pectinatus	Panicularia nervata

Scirpus microcarpus
Eleocharis glaucescens
Carex aurea
Carex disperma
Carex lanuginosa
Carex nebraskensis
Carex rostrata
Carex stipata
Juncus ensifolius
Juncus saximontanus
Batrachium trichophyllum
Ranunculus cymbalaria
Callitriche palustris
Steironema ciliatum
Veronica americana
Limosella aquatica

Mesophytic societies

Limnorchis hyperborea
Actaea arguta
Ranunculus macounii
Heuchera richardsonii
Vicia americana
Viola canadensis
Sanicula marylandica
Zizia cordata
Pyrola asarifolia
Moneses uniflora
Gentiana plebeja
Gentiana strictiflora
Prunella vulgaris
Stachys palustris
Castilleja sulphurea
Galium triflorum
Linnaea americana

The dominant birches and willows of the upper streamsides are partially replaced in the lower canyons by *Populus angustifolia*, *P. acuminata*, and *P. sargentii*. *Salix bebbiana* and *S. fendleriana* persist, and with them are found *S. balsamifera*, *S. fluviatilis*, and *S. lutea*. Intermixed with these are oak, elm, boxelder, ash, and plum, suggesting a gradual transition in the direction of the deciduous forest association.

The successional relationships of the streamside association can be interpreted variously. The dominants in the association belong to a developmental rather than to a climax stage; but there is a permanence to this type of plant community which might be considered as an indication of a climax or subclimax situation. A clue is afforded, however, in the occurrence of several of these dominants in an intermediate zone between the upland meadow and the montane forest (fig. 15). This indicates the true successional position as preclimax to the montane forest, at least in the upper stream phase. In the lower canyons the *Betula-Salix-Populus* association may be

considered as a subclimax, which under very favorable conditions will be replaced by the deciduous forest.

UPLAND MEADOW STAGE; GRASS-SEDGE ASSOCIATION.—The finest examples of the upland meadow are located in the northwest portion of the Limestone District. Here they reach their highest development, and exhibit the most luxuriant growth of meadow grasses and herbs to be found anywhere in the Hills. The present studies were

FIG. 15.—Meadow in Limestone District showing good zonation: marginal shrub *Salix bebbiana;* intermediate zone made up of *Populus tremuloides; Pinus scopulorum* in background.

made at three stations: (1) one mile east of the Hardy Ranger Station; (2) in the vicinity of Crooks Tower, 5 miles south of Mountain View Ranch; and (3) at the head of Castle Creek, 12 miles west of Deerfield.

The plateau is mesophytic, having an average annual rainfall of 21–25 inches. It has an elevation of 6500–7000 feet, and in consequence the snow remains in the meadow depressions late in the spring. These two factors operate together to supply sufficient moisture for the development of an abundant meadow flora. This reaches its most brilliant aspect in late June and early July, when the meadows are very colorful.

The meadow dominants are mainly grasses and sedges, with *Poa* predominating, but there are no outstanding groupings.

Dominants

Torresia odorata
Stipa richardsonii
Oryzopsis asperifolia
Phleum pratense
Agrostis hiemalis
Danthonia intermedia
Poa compressa
Poa fendleriana
Poa interior
Poa pratensis
Bromus marginatus
Bromus porteri
Agropyron repens
Elymus innovatus
Carex festivella
Carex hoodii
Carex tenera

Societies

Juncoides comosum
Juncus confusus
Iris missouriensis
Sisyrinchium angustifolium
Delphinium bicolor
Aconitum ramosum
Anemone globosa
Ranunculus cardiophyllus
Thalictrum venulosum
Sieversia ciliata
Astragalus alpinus
Oxytropis gracilis
Lupinus sericeus
Geranium viscosissimum
Viola adunca
Viola canadensis
Dodecatheon pauciflorum
Valeriana ceratophylla
Antennaria rosea
Rudbeckia hirta
Balsamorrhiza sagittata
Helianthella quinquinervis
Gaillardia aristata
Crepis riparia

The marginal zonation of the meadows is very clearly defined, and indicates the probable relationship of the meadow in the succession (fig. 15). The first zone beyond the meadow proper, when present, consists of low-growing shrubs: *Ceanothus velutinus*, *Dasiophora fruticosa*, and *Juniperus sibirica*. This is followed by a zone of willows, the principal species being *Salix bebbiana* and *S. scouleriana*. The outermost zone is made up of *Populus tremuloides*, which in turn makes contact with the climax yellow pine forest.

The meadow is thus a developmental phase leading up to the climax montane forest through the willow and aspen stages. Its

persistence can be attributed to edaphic factors and to the topography of the habitat. The former refer to the physical characteristics of the soil, which are unfavorable to the establishment of tree seedlings, as in the case of the prairie habitats previously discussed. The meadows invariably occupy basin-like depressions in which the snow accumulates and remains late in the spring. This condition favors the grasses and herbs, and makes invasion of the meadow by the forest an extremely slow process. Another restricting factor is the effect of continued grazing and haying, which prevents seedling development. The analysis of the causes for the permanency of the meadow community, which indicates that the factors at work are other than climatic, is the basis for the present classification of the upland meadow as a preclimax stage.

Xeric series

The early stages in the xeric succession are of three general types: (1) the rock pioneer, (2) the erosion pioneer, and (3) the secondary succession pioneer. The first is well illustrated by the plant communities found on the exposed summits of the mountain peaks, and on the rocky walls of many of the canyons. The second can be studied where the original vegetational cover has been destroyed by the erosive action of water and wind. The third is similar in aspect to the second, but is the result of different factors which are largely humanistic. These include overgrazing, road-building, and attempts at agriculture which are later abandoned.

Rock pioneer stage.—Studies of this stage were made at three points: (1) Harney Peak, elevation 7240 feet; (2) Terry Peak, elevation 7071 feet; and (3) Custer Peak, elevation 6794 feet. In each instance the summit is a rocky windswept habitat, where the climatic and edaphic factors are unfavorable to any but the hardiest pioneer plants. Rock lichens and mosses represent the earliest stages in the succession, common forms being *Placodium elegans*, *Rhizocarpon geographicum*, and *Grimmia*. Grasses and herbaceous crevice plants follow the lichen-moss stage, and are in turn replaced by crevice shrubs. These are followed by the subclimax birch and aspen, and ultimately the climax pine-spruce association is established.

Herbaceous crevice plants

Filix fragilis
Woodsia scopulina
Selaginella densa
Calamagrostis purpurascens
Danthonia spicata
Carex festivella
Carex siccata
Cerastium oreophilum
Sagina saginoides
Draba luteola
Arabis fendleri
Sedum stenopetalum
Drymocallis fissa
Drymocallis pseudorupestris
Androsace diffusa
Myosotis alpestris
Antennaria rosea

Crevice shrubs

Juniperus sibirica
Ribes cereum
Ribes irriguum
Ribes parvulum
Physocarpus monogynus
Rubus strigosus
Dasiophora fruticosa

Crevice plants found at lower elevations in the canyons include:

Polypodium hesperium
Cheilanthes feei
Pellaea glabella
Woodsia oregana
Aquilegia brevistyla
Aquilegia canadensis
Sophia pinnata
Parnassia parviflora
Heuchera hispida
Heuchera richardsonii
Tellima parviflora
Petrophyton caespitosum
Musineon tenuifolium
Antennaria aprica

EROSION PIONEER STAGE.—These stages are locally common wherever the work of water and wind has opened up a new habitat to invasion; but the most striking examples are located east of the Hills proper, in the White River Bad Lands, where the eroded surfaces of the Great Wall exhibit the first evidences of the xeric succession. Early pioneers in such habitats are:

Allium reticulatum
Eriogonum crassifolium
Eriogonum multiceps
Monolepis nuttalliana
Atriplex canescens
Lesquerella alpina argillosa
Pachylophus caespitosus
Lappula occidentalis
Oreocarya glomerata
Gutierrezia sarothrae
Grindelia squarrosa
Chrysothamnus graveolens
Chrysothamnus wyomingensis

These are followed by grasses of the mixed prairie, *Bulbilis*, *Koeleria*, *Sitanion*, and *Stipa* in the later stages of the succession.

SECONDARY SUCCESSION PIONEER STAGE.—In this stage, the first vegetation consists of ruderals. There are many situations illustrating this type of community, but one of the most clearly defined habitats occurs where the original cover has been destroyed by recent highway construction. The practice in widening the highways is to plow up a zone considerably wider than the actual highway, from which the top soil is scraped for grading purposes (fig. 11). This leaves an exposed strip on either side which is soon invaded by a characteristic group of annual plants.

Secondary succession annuals

Echinochloa crus-galli	Capsella bursa-pastoris
Panicum barbipulvinatum	Camelina sativa
Cenchrus pauciflorus	Cleome serrulata
Festuca octoflora	Medicago lupulina
Bromus japonicus	Euphorbia marginata
Bromus tectorum	Malva rotundifolia
Chenopodium album	Verbena bracteosa
Chenopodium paganum	Solanum rostratum
Salsola pestifer	Plantago purshii
Amaranthus retroflexus	Ambrosia elatior
Lepidium apetalum	Dysodia papposa

These annuals are followed by deep-rooted perennials such as *Gutierrezia sarothrae*, *Yucca glauca*, *Malvastrum coccineum*, *Grindelia perennis*, *Artemisia frigida*, *Brauneria angustifolia*, *Ratibida columnaris*, *Petalostemon purpureus*, and *Eriogonum multiceps*. The perennials form an open cover, and the entry of the grasses of the mixed prairie follows, completing the succession.

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RHIZOCTONIA DISEASE ON CERTAIN AQUATIC PLANTS[1]

W. S. Bourn and Bernice Jenkins

(plates xi–xiv and six figures)

Introduction

The inland waters of Back Bay, Virginia, and Currituck Sound, North Carolina (fig. 1) have long been known to represent one of the most important winter feeding grounds for migratory wild fowl in the United States. Here aquatic duck-food plants, such as *Potamogeton pectinatus* L., *P. perfoliatus* L., *Ruppia maritima* L., *Vallisneria spiralis* L., and *Naias flexilis* (Willd.) Rostk. & Schmidt formerly thrived in great abundance. In 1918, almost simultaneously with the opening and enlargement of the Albemarle and Chesapeake Canal, however, these plants began to die out, and by the end of 1926 vast areas were practically denuded of their aquatic vegetation. This destruction of the plant life has wrought an enormous economic loss upon thousands of the native population, who derived their living from gunning and fishing. Shooting clubs and sportsmen have practically deserted their large investments in the region, since wild ducks and geese in any appreciable numbers are no longer attracted there. At the request of William E. Corey, a prominent sportsman of New York, who has been interested in these waters, the Boyce Thompson Institute for Plant Research in 1925 undertook a study of the causes for the disappearance of the aquatic duck-food plants, and early the following year the writers were assigned to the investigation.

The region involved represents an area of approximately 300 square miles of inland waters. At 26 widely scattered stations in this area, periodic analyses have been made to determine the salinity of the water. Field observations have been made almost daily from March to October. Plant specimens have been collected for study

[1] Contributions from the Boyce Thompson Institute for Plant Research, Inc., Yonkers, New York, published at the expense of the Institute out of the order determined by the date of receipt of the manuscript.

at various stages of growth and decay. Experiments to determine the influence of soil, water, and salinity upon the growth and the disease of aquatic plants native to the region have been carried on for more than two years in the greenhouse. Inoculation experiments,

FIG. 1.—Map of Back Bay, Virginia, and Currituck Sound, North Carolina, regions.

using cultures of a fungus isolated from diseased aquatic plants and from diseased potato plants, have extended over the same period of time.

While other injurious factors have been encountered during the course of the investigations, it is the purpose of this paper to describe and discuss a *Rhizoctonia* disease which we believe to be the

factor of greatest importance, and the one most directly responsible for the disappearance of the aquatic duck-food plants in Back Bay and Currituck Sound.

The fungus *Rhizoctonia solani* Kühn is widely distributed in America and elsewhere, having been reported from most regions of the world where the potato is a staple crop. In addition to the potato, which appears to be the most common host, the host plants of this fungus represent many families of dicotyledons and a number of monocotyledons. PELTIER (4) lists about 165 species of plants susceptible to *R. solani*. PALO (3) has recently reported this fungus causing a serious disease of rice in the Philippines. Regardless of the multitude of host plants reported in the literature, which we shall not attempt to review, the occurrence of *Rhizoctonia* on rice plants, to our knowledge, is the closest approach to an occurrence on aquatic plants thus far reported. When we consider such a wide range of hosts, and the fact of its occurrrence on semi-aquatic plants, the discovery of *R. solani* in a purely aquatic situation is less surprising, if unusual.

L. O. KUNKEL, pathologist of the Boyce Thompson Institute for Plant Research, first isolated pure cultures of *Rhizoctonia solani* from diseased aquatic plants collected from Back Bay, Virginia, in September 1925. Since that time we have repeatedly isolated pure cultures of this fungus from diseased plants collected from the infected area. We have inoculated plants growing in the greenhouse aquaria with sclerotia from these cultures. These inoculated plants became infected almost immediately, and later pure cultures of the fungus were re-isolated from them. We have determined that this aquatic strain of *Rhizoctonia* will not only kill aquatic plants but will also attack such terrestrial plants as the potato; furthermore, that a strain of *R. solani*, isolated from diseased potato plants, will attack aquatic plants.

Occurrence and identification of Rhizoctonia on diseased and dead tissue

In the field it was noticed that signs of *Rhizoctonia* infection first became visible as dark lesions on portions of the plant stems, near the first node at the surface of the soil. Infection took place on this

portion of the plant regardless of the depth of the water in which the plant was growing. By taking one-fourth inch segments of these diseased stems, washing them half a dozen times in several cubic centimeters of sterile distilled water, to remove water bacteria, etc., and then tranferring these segments to potato and to green string bean agar, pure cultures of *R. solani* were obtained. After the segments had been in the agar one to two days, the fungus could be observed growing out into the agar from the cut ends of the segments. At the end of the fourth day the growth was about the size of a half-dollar, and very shortly thereafter the entire plate became covered by the mycelial growth. About the second week small white spots, 1–2 mm. in diameter, appeared in the older mycelia near the center of the agar plates. Within a few more days these white spots became the black sclerotia shown in pl. XI. Concentric zonations are characteristic of these cultures, and showed plainly in most of them. In measurements of hyphal and sclerotial cells, in mycelial and cultural characteristics, and in physical appearances this fungus corresponds closely to the descriptions of *R. solani* given in the literature. The aquatic strain and the potato strain of *Rhizoctonia* are compared in the cultures shown in pl. XI. *A* and *B* are cultures of the fungus isolated in 1926 from diseased aquatic plants collected from Back Bay, on potato agar and on green string bean agar respectively; *C* and *D* are cultures on potato and green string bean agar respectively of the aquatic strain of *Rhizoctonia* re-isolated in 1927 from greenhouse aquatic plants used in the inoculation experiments; *E* and *F* represent cultures of *R. solani* isolated from diseased potato plants, on potato and on green string bean agar respectively.

Inoculations with Rhizoctonia; production of the disease; subsequent re-isolation of the fungus

To determine the effects of *Rhizoctonia* inoculations upon five species of aquatic duck-food plants, *Potamogeton pectinatus, P. perfoliatus, Ruppia maritima, Vallisneria spiralis,* and *Naias flexilis,* experiments were set up in the greenhouse aquaria. In these experiments four types of soil were used. Water solutions were made up by diluting boiled Long Island Sound water with distilled water

until the solutions contained a saline content equal to the average for Back Bay, to one-half, and to double that concentration. Ten gallons of water was used in each culture. This furnished two feet of water over six inches of soil in the vessels. The form of the plants used in these cultures was either seeds, tubers, or young plants. Inoculations were made by placing in the soil sclerotia of the strain of *Rhizoctonia* isolated from Back Bay aquatic duck-food plants. The results obtained for the inoculation cultures, using *Potamogeton pectinatus*, are given in table I.

TABLE I

RESULT OF INOCULATION OF POTAMOGETON PECTINATUS WITH AQUATIC STRAIN OF RHIZOCTONIA SOLANI

Soil	Salinity of water in percentage of normal sea water	Average length of plant life	
		Inoculated	Check
Sterile quartz sand	3.5	45 days	100 days
Sterile quartz sand	7.0	20 days	100 days
Sterile quartz sand	14.0	35 days	90 days
Sterile Back Bay soil	3.5	No growth*	No growth*
Sterile Back Bay soil	7.0	No growth*	No growth*
Sterile Back Bay soil	14.0	No growth*	No growth*
Untreated Back Bay soil	3.5	40 days	200 days
Untreated Back Bay soil	7.0	25 days	100 days
Untreated Back Bay soil	14.0	30 days	100 days
Sterile garden soil	3.5	40 days	2 years
Sterile garden soil	7.0	30 days	2 years
Sterile garden soil	14.0	30 days	2 years

* Failure of growth due to iron bacteria which grew so abundantly that growth of other plants was prevented.

For the experiments with the other four species of plants mentioned, no tabular results are given. These experiments were set up later and all the checks are still living. The average length of life of the inoculated plants, however, approximates the averages given for *Potamogeton pectinatus*, with the exception of *Vallisneria spiralis*. The absence of a stem above the ground in this plant aids in the prolongation of life, as it is necessary for the fungus to destroy the dozen or more leaves before the plant dies. This plant lived in the inoculated cultures from two to several weeks longer than the species of *Potamogeton*. From the diseased plants of these experiments pure cultures of *Rhizoctonia solani* were re-isolated.

The preceding experiments were run in duplicate with a strain

of *Rhizoctonia* isolated from diseased potatoes. No appreciable differences were observed, however, between the results of these experiments and those in which the aquatic strain of the fungus was used for the inoculations.

Relation of salt content of water to incidence of the disease

In order to determine the influence of different degrees of salinity of the water upon the *Rhizoctonia* disease, tubers of *Potamogeton pectinatus* were cultured in glass museum jars with boiled Long Island Sound water diluted with distilled water to the following concentrations: no sea water, 3.5, 7.0, 10.5, 14.0, 17.5, 20.0, 25.5, 27.0, 30.5, and 40.0 per cent normal sea water. The concentrations were checked by the titration method described by DENNY (1). No soil was used in this experiment. Three tubers were cultured in each jar, the tubers being weighted down by sterile stones (pl. XII). One of the tubers was inoculated by making a slight cut and inserting sclerotia of the fungus in the wound; a second tuber was inoculated merely by tying sclerotia on to it; the third tuber of each culture was not inoculated. For these inoculations the aquatic strain of *Rhizoctonia* was used. Duplicate experiments were run, using for the inoculations pure cultures of *Rhizoctonia* isolated from diseased potato plants.

Rhizoctonia isolated from aquatic plants was found to attack the plants in all salt concentrations employed in the experiment. The disease appeared more virulent, however, in those concentrations between 7 and 20 per cent normal sea water. In none of these cultures did plants live longer than six weeks. All three tubers of each culture became equally infected; injuring the tuber apparently did not aid the infection.

Pl. XII shows four plants two weeks after inoculation with the aquatic strain of *Rhizoctonia*. *G* is a plant cultured in fresh water; *H* in 3.5 per cent normal sea water; *I* in 7 per cent sea water (the concentration of Back Bay); and *J* in 14 per cent sea water. Pl. XIII shows plants of the same cultures, in the same order, four weeks after inoculation. Photographs for these plates were taken through the museum jars and the water solutions in which the plants were cultured.

The strain of the fungus isolated from diseased potatoes attacked the plants in all concentrations used in the experiment. The disease induced by this strain, however, was most destructive to the plants cultured in fresh water and in the concentrations below 10.5 per cent sea water. While plants cultured in the higher concentrations were attacked, death did not occur until long after the plants had fruited. In pl. XIV, *O* represents plants of a 10.5 per cent normal sea water culture; *P* those of a 27 per cent normal sea water culture. Both photographs were taken three weeks after inoculation with *Rhizoctonia solani* isolated from diseased potato. The facts that this strain of the fungus attacks aquatic plants growing in salt solutions of lower concentrations and that the aquatic strain attacks those in the higher concentrations indicate that the two are separate physiological strains of *Rhizoctonia*.

Effect of aquatic strain of Rhizoctonia upon potatoes

In order to make a more complete comparison between the potato and the aquatic strains of *Rhizoctonia*, it now remained to study the effects of the aquatic strain upon potato plants. For this purpose potatoes were grown in sterile soil under bell jars. A part of the seed pieces were inoculated in the eyes, at the time of planting, with sclerotia of the fungus. Other inoculations were made in the stems of plants just beneath the surface of the soil. Within a short time dark brown lesions, or sunken areas, appeared on the stems of the inoculated plants, and many underground stolons were completely severed. Upon the appearance of the stem lesions the bell jars were removed and the plants were left to grow for several weeks, until tubers had formed. Upon examination, sclerotia of the fungus were discovered on these tubers, many of which were badly scabbed and russeted (fig. 2).

The results obtained in all the preceding experiments with the two strains of the fungus check very closely. For this reason, there is a possibility that the aquatic plants in Back Bay and Currituck Sound have become infected with *Rhizoctonia* from diseased potatoes. While a large district in which potatoes are grown on a commercial scale drains into these waters, and *Rhizoctonia* is known to occur in these potato fields, we do not know that this is the source of

infection. There seems to be just as strong a possibility that the source of the fungus may be found in the great amount of sewage that enters these waters from the city of Norfolk by way of the Albemarle and Chesapeake Canal.

Seasonal developments of the disease

Evidences of *Rhizoctonia* infection are usually observed each year during the first half of June on the *Potamogeton pectinatus* plants growing in the northern part of Currituck Sound and in Back Bay.

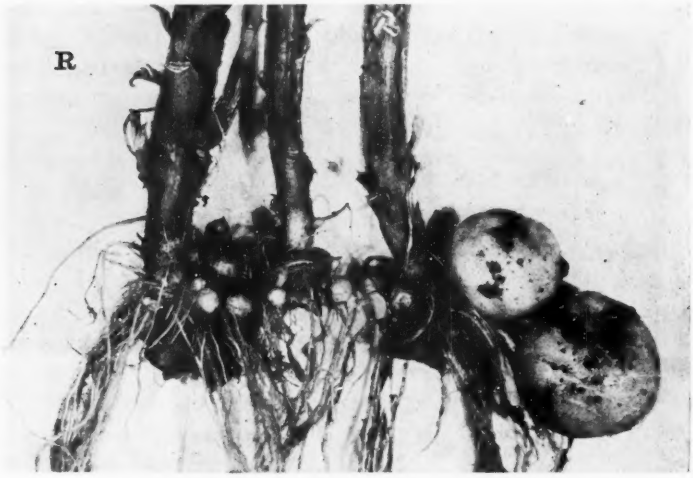

FIG. 2.—Effect of aquatic strain of *Rhizoctonia* upon potatoes

During this month these plants are rather well covered by gelatinous remains of old hydroid colonies which infest the plants a little earlier in the season. At this time of the year the *Rhizoctonia* infections are somewhat limited to dark brown lesions on lower portions of the plant stems, but during the warmer months of August and September the effects of the disease become quite marked in the entire appearance of the plant. We have been able to isolate pure cultures of the fungus from these diseased plants in the months of June, July, August, and September. During the months of August and September the salinity of the water is usually highest (fig. 3). Great

areas of the plants, which up to this time of the season have appeared green, become brown and die within a few days. While the increased salinity of the water may lower the resistance of the plants to the disease, it can hardly be said to kill them, for we have been able to grow the same plants in much saltier water than that found in Back Bay. Furthermore, the dead areas of plants are usually very

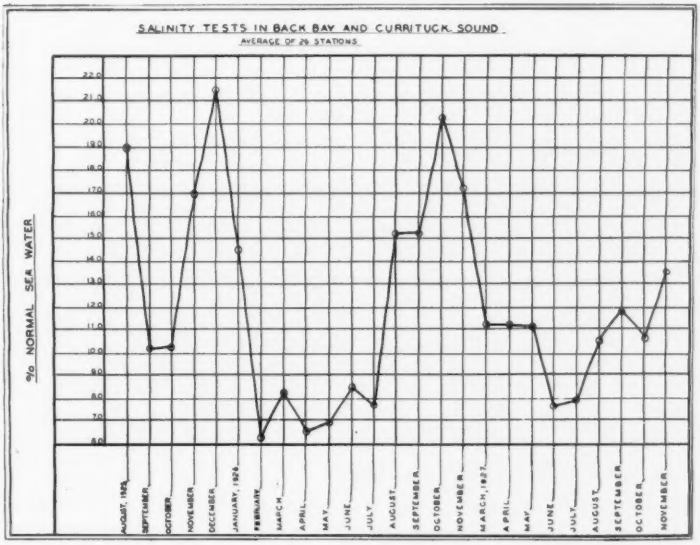

FIG. 3.—Graph showing results of monthly salt analyses of waters of Back Bay and Currituck Sound; readings in percentage of normal sea water, representing averages for 26 widely scattered stations in the region.

irregular, and injuries are restricted to definite portions of the plant itself.

The depth of the water does not effect the development of the disease. *Rhizoctonia* has been found to attack the plants growing in all depths found in Back Bay and Currituck Sound. The depth of these waters, however, does not usually exceed ten feet. In this region there is considerable wind and wave action, and diseased plants, which have lost their anchorage, are easily washed from one area to another. Plants more or less isolated are easily broken off

after infection at the surface of the soil, and are washed ashore while still green; but where the growth is denser the plants remain attached and sink to the bottom after complete decay. In the greenhouse inoculation experiments the plants probably remained attached and alive much longer than they would have done in nature, because wave and wind action was not encountered.

Susceptibility of different plants to the disease

While *Rhizoctonia* has been found to attack most of the species of duck-food plants in Back Bay and Currituck Sound, *Potamogeton pectinatus*, which is the dominant plant of the region, and, incidentally, the most valuable duck-food known, is the most susceptible to the disease. This species is the first to make a growth in the spring, and usually reaches the surface of the water, even in the greater depths, before growth begins in other species of duck-food plants mentioned. Isolated areas of *Vallisneria* and *Naias* do not readily become infected with the disease, but infection does occur when these plants are associated with *Potamogeton*. Next to *P. pectinatus*, the plant most susceptible to the disease is *Ruppia maritima*. In this locality the *Ruppia* zone, while in shallower water, usually overlaps the *Potamogeton* zone. Because of its ease in vegetative propagation, however, *Ruppia* usually survives where the *Potamogeton* dies. Plants of all species studied seem less susceptible to the disease when growing, somewhat sheltered from the winds, in sandy soil.

Mycelial and sclerotial characteristics of fungus

A microscopic examination, as well as a cultural isolation, of the infected portions of the plants reveals hyphae of *Rhizoctonia*. Under natural conditions mycelial threads are seldom so abundant as to be discernible by the naked eye, but are quite visible in aquaria cultures (pls. XII and XIII). The older external hyphae (fig. 4) are somewhat colored, usually a uniform yellowish brown, with branches arising at approximate right angles to the main hypha; the internal hyphae are usually smaller, practically colorless, and the branching is more or less dichotomous. The younger hyphal branches (fig. 5) are practically colorless and contain large globules. Microchemical tests indicate that these globules contain glycogen. The hyphal

branches are almost invariably constricted, and contain a septum near the point of union with the main hypha (figs. 4, 5). The size of the mycelial cells, taken from 100 measurements, is 50–225×5.50–12 μ. DUGGAR (2) gives 100–200×8–12 μ for the size of the hyphal cells of *Rhizoctonia solani*. PELTIER (4) found the size of the hyphal cells of the different strains of the fungus was 65.24–5.01–6.57 μ,

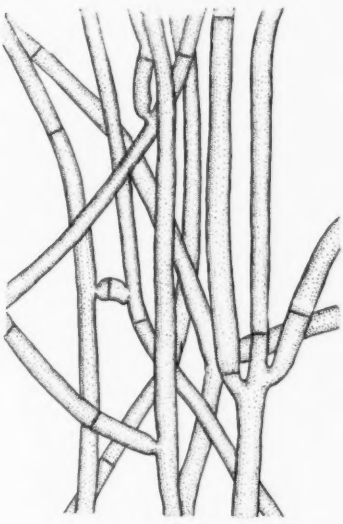

FIG. 4

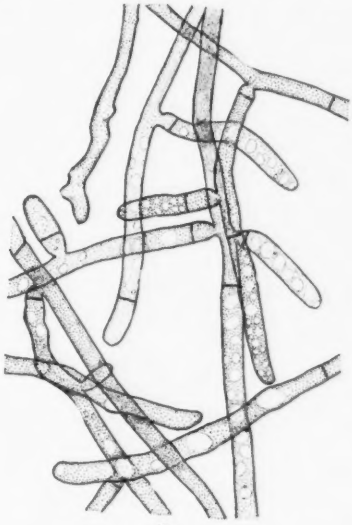

FIG. 5

FIGS. 4, 5.—Fig. 4, *Rhizoctonia solani*, camera lucida drawing of portion of mycelium growing on aquatic plant; fig. 5, *Rhizoctonia solani*, camera lucida drawing of young hyphal branches of mycelium growing on aquatic plant.

but gave for the length of the cells of the strain parasitic upon *Dianthus* 50–215 μ. PALO (3) states that the measurements of the hyphal cells of the strain parasitic upon rice are 24–248×4–12.8 μ. The majority of our measurements for the aquatic strain fall within the range given by DUGGAR.

Hyphae of the infecting mycelia readily penetrate the tissues of the aquatic plants. These penetrating hyphae appear greatly swollen at points of entry or exit from the cells of the host tissue, but a very constricted portion of the hyphae penetrates the cell walls of the host plant.

The exact conditions under which sclerotia may occur on the plants in their native habitat have not been determined. Sclerotia have been observed on the dead plants which float ashore in the late summer. In pl. XIV, *Q* is a photomicrograph of a small stem of an aquatic plant containing sclerotia of the fungus. This plant was fixed in chrom-acetic fixative and stained *in toto* with eosin and Ehrlich's haematoxylin. Sclerotia first appear on the plants which have washed ashore as light spots bordered by a dark brownish ring of discolored host tissue. These light spots later become dark specks. Some of the sclerotial cells are irregular, flattened, dark, and more or less granular in structure; others, especially of the loose hyphae covering the sclerotia, are barrel-shaped, less colored, and are vacuolate (fig. 6). It is assumed that the sclerotia overwinter in the muck and débris at the bottom of the water. PALO, in reporting the occurrence of *Rhizoctonia solani* upon Philippine rice, states that the viability of the sclerotia is destroyed after its submergence in water for a period of two to three months. We have succeeded in obtaining infection without re-inoculation in aquaria two years after the soil in these vessels had been inoculated with sclerotia of the aquatic strain of *Rhizoctonia*. This may be due to a prolonged mycelial growth of the fungus, however, as we were unable to determine that sclerotia had formed in the aquaria.

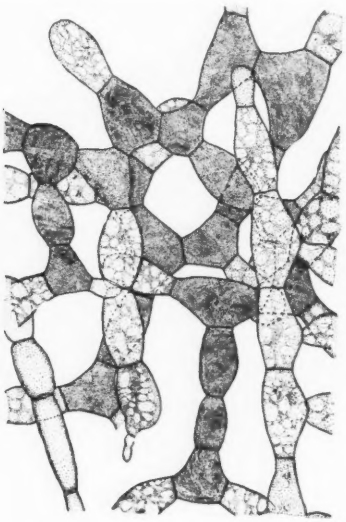

FIG. 6.—*Rhizoctonia solani;* sclerotial cells found on aquatic plant; camera lucida drawing made from stained specimen.

Summary

1. Great areas of aquatic duck-food plants have been destroyed in Back Bay, Virginia, and Currituck Sound, North Carolina. Di-

rectly or indirectly, this has caused a large economic loss to a large population. A fungus disease has been found the factor most responsible for this loss.

2. Pure cultures of a strain of *Rhizoctonia* have been repeatedly isolated from diseased aquatic duck-food plants collected from the infected waters. A disease, identical with that produced by a strain of *R. solani*, has been produced in greenhouse aquaria plants by inoculations with this aquatic fungus. Pure cultures of the fungus have again been re-isolated from these greenhouse plants. Moreover, a disease has been produced on potato plants by inoculating the plants with sclerotia from culture of this aquatic fungus.

3. This aquatic strain of *Rhizoctonia* has been found to attack five species of aquatic duck-food plants: *Potamogeton pectinatus*, *P. perfoliatus*, *Ruppia maritima*, *Vallisneria spiralis*, and *Naias flexilis*. Attacks have occurred on plants growing in various types of soils, and in waters containing a wide range of salt content. Muck soils and a salinity of 7–20 per cent normal sea water, however, are most favorable for the growth and activity of the fungus. These suitable conditions of soil and salinity now exist in Back Bay and Currituck Sound.

4. Morphological and cultural characteristics indicate that this fungus is a physiological strain of *Rhizoctonia solani*, and it is so considered by the writers.

5. To our knowledge, this is the first case ever reported of the occurrence of *Rhizoctonia solani* on aquatic plants.

6. A strain of *Rhizoctonia solani* isolated from diseased potatoes has been found to attack aquatic plants growing in various types of soils and salt solutions. This disease was identical with that produced by the aquatic strain of the fungus, but occurred in lower salt concentrations.

7. Under favorable conditions *Rhizoctonia solani* is an aggressive parasite upon those species of aquatic plants studied in this investigation, and the disease induced by it has caused much damage to these plants growing in the infected waters.

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YONKERS, NEW YORK

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EXPLANATION OF PLATES XI–XIV

PLATE XI

Three weeks' old cultures of *Rhizoctonia solani: A* and *B*, cultures of fungus isolated in 1926 from diseased aquatic plants collected from Back Bay, on potato agar and on green string bean agar respectively; C and *D*, cultures on potato and green string bean agar respectively, of aquatic strain of *Rhizoctonia* re-isolated in 1927 from greenhouse aquatic plants used in inoculation experiments; *E* and *F*, cultures of *R. solani* isolated from diseased potato plants, on potato and on green string bean agar respectively.

PLATE XII

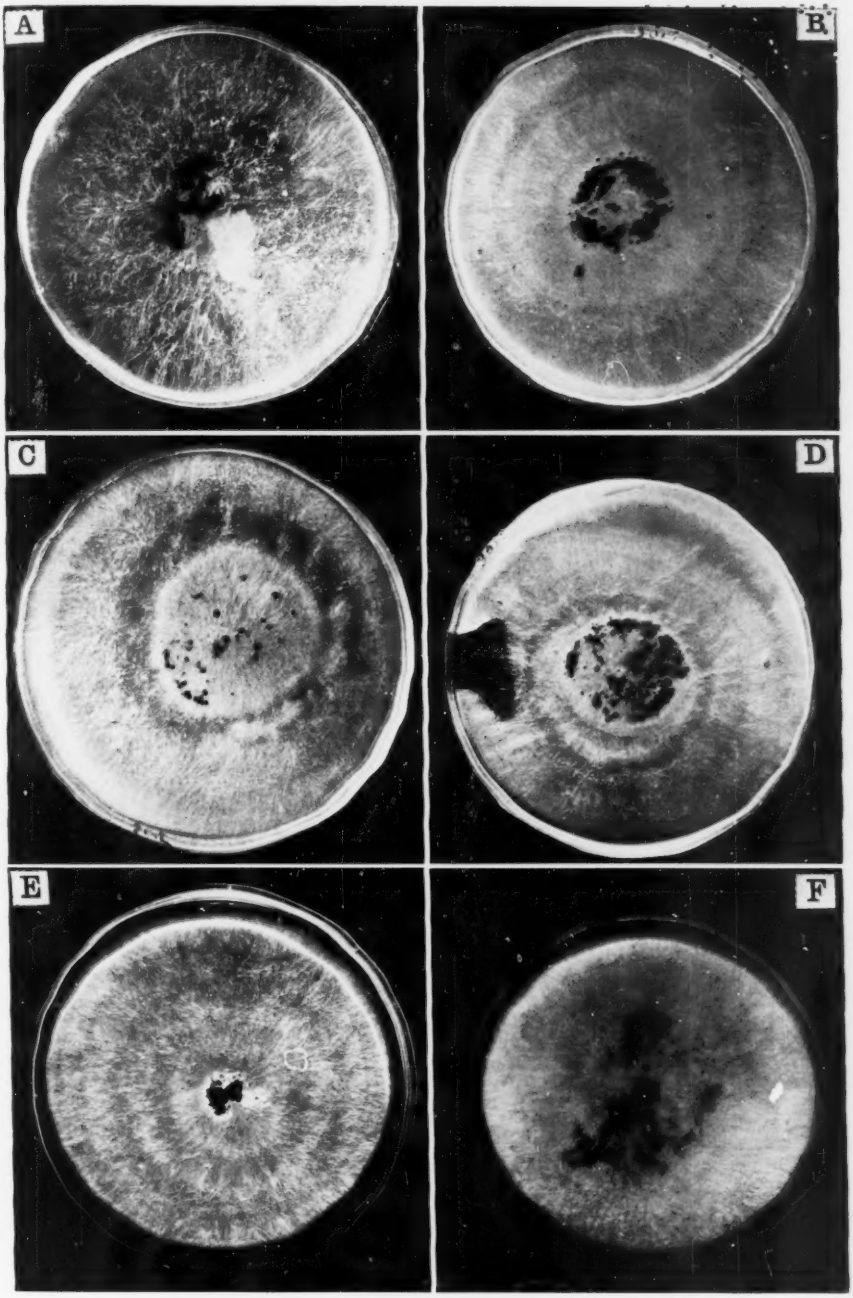
Potamogeton pectinatus plants two weeks after inoculation with sclerotia of aquatic strain of *Rhizoctonia; G*, plant cultured in fresh water; *H*, in 3.5 per cent normal sea water; *I*, in 7 per cent.

PLATE XIII

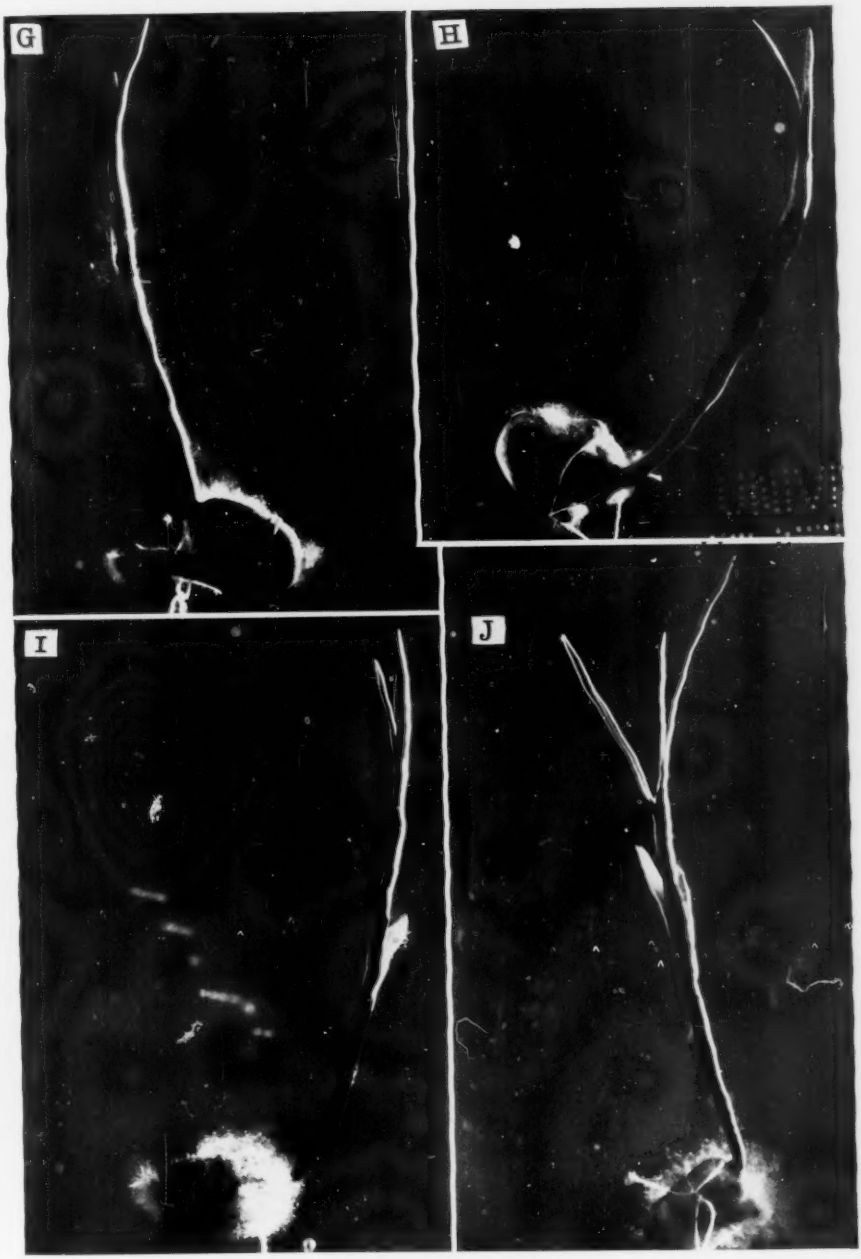
Same as pl. XII four weeks after inoculation; these are plants from the same cultures and arranged in same order as in pl. XII.

PLATE XIV

Potamogeton pectinatus plants (*O*) growing in 10.5 per cent normal sea water three weeks after inoculation with sclerotia of *Rhizoctonia* isolated from diseased potato plants; *P*, same as preceding except plants are growing in 27 per cent sea water; *Q*, photomicrograph of sclerotia of aquatic strain of *Rhizoctonia* on small stem of *P. pectinatus;* plant found washed ashore in Back Bay, Virginia; specimen fixed in chrom-acetic fixative and stained with eosin and Ehrlich's haematoxylin.



BOURN & JENKINS on RHIZOCTONIA



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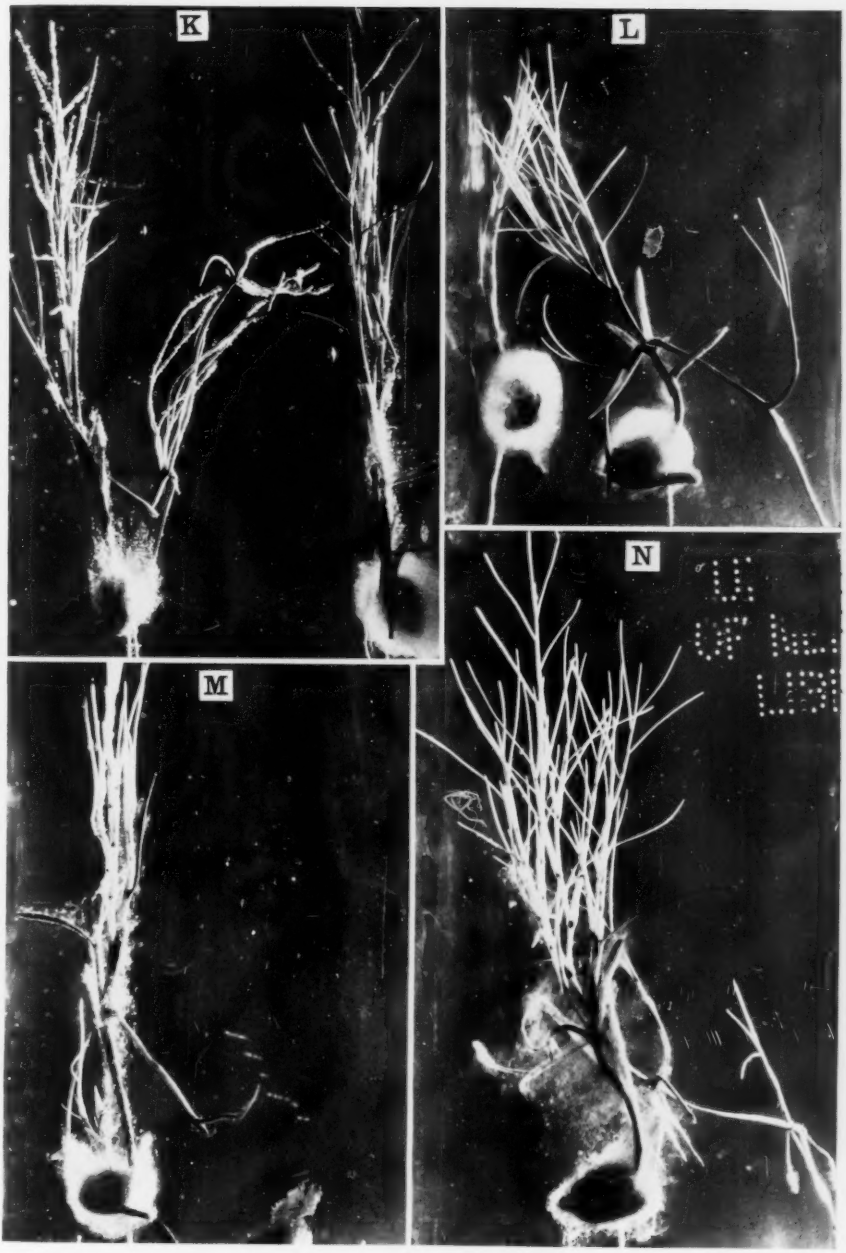

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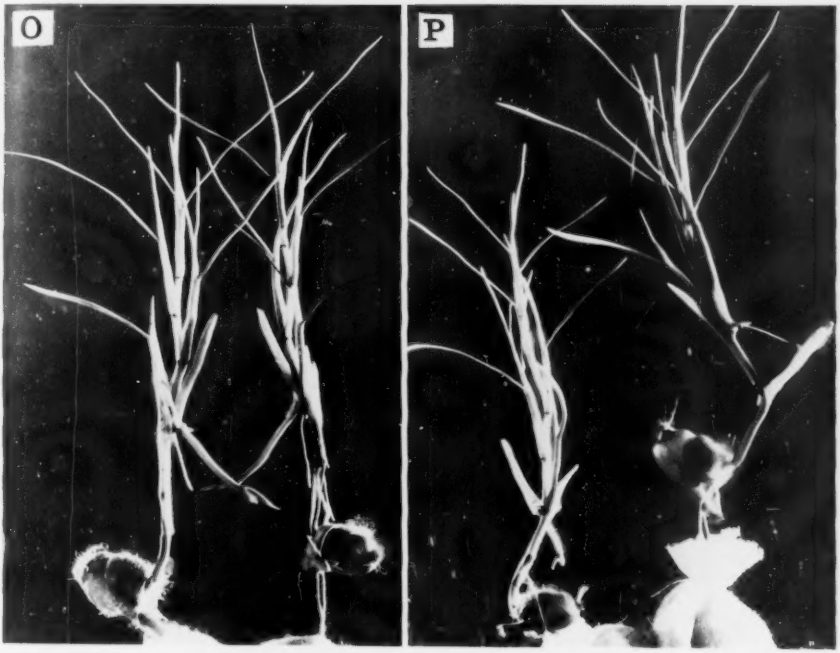

Q

BOURN & JENKINS on RHIZOCTONIA

ANATOMICAL STUDY OF PLANTS GROWN UNDER GLASSES TRANSMITTING LIGHT OF VARIOUS RANGES OF WAVE LENGTHS[1]

NORMA E. PFEIFFER

(WITH PLATES XV–XVIII AND ONE FIGURE)

A series of plants was grown in glass houses at Boyce Thompson Institute for Plant Research in the summer of 1927, for physiological experiments. A few of the plants were available for anatomical study, the results of which are here recorded. The houses in which the plants were grown have been previously described and figured by POPP.[2] Briefly, each house is 9×11 feet, with roof sloping to the south, with a difference of 2 feet in height at front and back of benches. The ventilation system is of the positive pressure type, electrically driven, with separate air intakes in each house and separate roof ventilator outlets. This results in temperatures which are approximately similar throughout the line of houses, although not identical with that existing out-of-doors in full sunlight.

Transmission of glasses used in houses

The glasses used in the houses in this experiment transmit light in the visible spectrum and in the ultra-violet in various ranges of wave length. The designations used for these houses, the trade name of the glasses,[3] and the ranges of each within these two spectral regions are as follows:

		Millimicrons
Visible-spectrum house	Noviol O	720–390
Full-spectrum house	Corex	720–290
Blue house	G403ED	585–335
Minus-violet house	Noviol C	720–471
Red house	G 34	720–526

[1] Contributions from the Boyce Thompson Institute for Plant Research, Inc., Yonkers, N.Y., published at the expense of the Institute out of the order determined by the date of receipt of the manuscript.

[2] POPP, HENRY W., A physiological study of the effect of light of various ranges of wave length on the growth of plants. Amer. Jour. Bot. 13:706–736. 1926.

[3] Corning glasses.

The spectrum of sunlight in the same regions is from 720 to 400 millimicrons in the visible spectrum, and from 400 to 290 millimicrons in the ultra-violet. The light in the full-spectrum house most nearly approaches this in quality of rays, transmitting the ultra-violet rays to the extent of about 80 per cent of their value in full sunlight. The blue house is limited in transmission in the visible spectrum to some yellow, green, and blue, with less rays in the ultra-violet than window glass transmits. The minus-violet house allows the passage of the red, yellow, green, and part of the blue of the visible spectrum. In the red house, only red, yellow, and part of the green of the visible spectrum are transmitted. The last two houses mentioned lack all ultra-violet rays, the visible-spectrum house most of them, and the blue house glass transmits less than window glass. Thus all four fail to transmit the rays valuable to higher animals because of their antirachitic effects. The blue and red house glasses transmit in common only some yellow and some green rays.

In addition to these five glass houses, two other locations served for comparison. One was an adjacent platform, commonly termed "outdoors," where plants received full insolation. Another was a "shade" house, a light frame structure covered with a double layer of gauze. This stood between the spectral glass houses and the "outdoors" plants, also having a southern exposure. These two situations did not have the similarity of temperatures that obtained in the glass houses.

Intensities

The measurements of intensities are those made by J. M. ARTHUR and H. L. SHIRLEY, using the Macbeth illuminometer and a pyrheliometer. The latter records radiant energy in terms of heat; the former is more specifically a measure for illumination. It is not entirely satisfactory, however, in that the eye, by means of which intensities are gauged, is not ideal in its ability to distinguish degrees of difference equally in various regions of the spectrum. Moreover, the color effect within the glass houses makes accurate readings even more difficult. Neither instrument records light in terms of the plant and physiological effects. Table I represents the averages of readings made at various times, based on the two methods. The light outdoors in each case was considered as 100 per cent intensity,

whether in terms of foot candles (Macbeth illuminometer) or millivolts (pyrheliometer).

Anatomical studies

From the range of plants available in the different sets of conditions, several were selected for a study of the anatomical effects produced by the light factor. So far as possible, plants had been grown from seed, although when necessary small plants, as 1-inch salvias, represented the stage at the beginning of the experiment. In all cases 2-gallon jars with forest soil were used for the plants. The beginning date of the experiment was June 13, 1927.

TABLE I

INTENSITIES IN THE VARIOUS SITUATIONS

SITUATION	MACBETH ILLUMINOMETER Per cent	PYRHELIOMETER Per cent
Outdoors	100	100
Visible-spectrum house	59.8	52.7
Full-spectrum house	55.0	50.8
Blue house	8.6	8.0
Minus-violet house	50.7	33.2
Red house	31.3	30.2
Shade house	16.2	23.2

STEMS.—When the plants were six weeks old, the stems of a number were examined, especially *Mirabilis jalapa*, *Brassica rapa* (Henderson's Purple Top White Globe), *Helianthus cucumerifolius* (type of Henderson), and *Glycine soja* var. *biloxi*. The first two proved least satisfactory for accurate comparison of degree of development of vascular tissues, because of the scattered arrangement of unequal bundles in four-o'clock, and because of the short stem in turnip which makes it difficult to get comparable preparations. Yet it was possible to see in these the same general effects that were more readily demonstrable in the typically dicotyledonous stems of the sunflower and soy bean. Later collections, made when the plants were approximately fourteen weeks old, again included these two forms.

Free-hand sections were made of the stem at the base and just below the middle node. These show similar trends, as may be seen in the illustrations from photomicrographs, taken at the fourteen-week

stage (pls. XV–XVIII). Study was made of two stems, of which one set was photographed. In comparing results, the full-spectrum house is considered the control, since it has the spectrum of sunlight and the temperature is similar to that of the other four houses. The different temperature outdoors and in the shade house bring in another factor which would eliminate the use of these as checks.

In soy bean (pls. XV and XVI) the stem in the full-spectrum house compares very favorably with that outdoors, and is noticeably stronger in development of woody tissues than in any other house. The plants in the shade house and minus-violet house are much alike, both a little less strong than those of the visible-spectrum house. Undoubtedly the plants in the blue and red houses represent the weakest development. That the least differentiation occurs in the blue house may be due as much to the very low intensity as to the special rays which reach the plant.

In the case of the sunflower (pls. XVII and XVIII) the full-spectrum house plant is not so strong in development of differentiated tissues as either the outdoors plant or that of the visible-spectrum house. There is little difference in intensity in the two houses, but that little is in favor of the visible-spectrum location. Whether this could be of more importance to a "sun" form like *Helianthus* than to other types, it is impossible to say. The plants in the minus-violet house also had well developed xylem, although here intensity is less high. It would have been interesting to compare the shade form in this case, but unfortunately all plants were used before the final anatomical study. The earlier stage showed weaker vascular tissues under these conditions than the minus-violet plants. In all cases the plants in the blue and red houses were least differentiated. In the upper region the former showed no secondary wood, although at a corresponding level the latter had a fair amount. With the low intensity in the blue room, it is very possible that the material for elaborating differentiated tissues is lacking. It is conceivable that the available food may be the limiting factor, and that the quality of light is not directly responsible for such weak development. Certainly the appearance of the plant, a sort of miniature of those in the full-spectrum house, is more nearly normal than that of plants in visible-spectrum, minus-spectrum, or red houses.

Aside from the actual amount of differentiated tissues produced, the dimensions of the stem prove of some interest. Considering the diameter of the base of the stem of the full-spectrum house as 100 per cent, we get the results shown in table II. Here the sunflower and four-o'clock appear to respond in similar fashion, with the exception of sunflower in the outdoors situation. Compared with these two, the soy bean makes a better showing, so far as diameter is concerned, in both the red house and in shade. This is not necessarily due to development of differentiated tissue, but chiefly to pith.

TABLE II

DIAMETER OF BASE OF STEMS (SIX WEEKS OLD) AS COMPARED WITH FULL-SPECTRUM HOUSE

House	Four-o'clock Per cent	Sunflower Per cent	Soy bean Per cent
Outdoors	95	150	97
Visible-spectrum	82	81	70
Full-spectrum	100	100	100
Blue	56	50	60
Minus-violet	78	75	70
Red	43	49	67
Shade	66	74	83

It is well to associate height with diameter. In table III the same plants considered in the previous table are listed on this basis, again with the full-spectrum plant as 100 per cent. Here also sunflower and four-o'clock appear more nearly parallel, whereas soy bean reacts quite differently. It endures low intensities better than the other two forms, as shown by diameter and height. On the other hand, where abnormal form is brought about by lack of the blue and ultra-violet rays, soy bean is even more affected (as shown by twining) than the other two genera.

Table IV records a comparison of heights from the more extensive physiological data collected by J. M. ARTHUR. The previous table is based on two samples, while this is an average of a greater number (2 to 7 more) of plants. In table V there is the same general trend, although minor differences appear in the figures.

LEAVES.—In form the leaves in the minus-violet and red houses appear puffed and warped, although they are ordinarily of very good

size. In the blue-house plants, on the other hand, the greatest reduction in leaf expanse runs parallel to the small size of the whole organism. The leaves in the other houses, which are intermediate between these two extremes, fall into this order, on the basis of expanse: second largest in visible and full-spectrum houses, next in outdoors and shade houses.

TABLE III

HEIGHT OF STEMS (SIX WEEKS OLD) AS COMPARED WITH FULL-SPECTRUM HOUSE; SAME STEMS AS TABLE I

HOUSE	FOUR-O'CLOCK Per cent	SUNFLOWER Per cent	SOY BEAN Per cent
Outdoors	85	85	57
Visible-spectrum	104	100	144
Full-spectrum	100	100	100
Blue	57	26	91
Minus-violet	100	110	181
Red	110	49	185
Shade	54	66	115

TABLE IV

AVERAGE HEIGHT OF STEMS (SIX WEEKS OLD) AS COMPARED WITH FULL-SPECTRUM HOUSE

HOUSE	FOUR-O'CLOCK Per cent	SUNFLOWER Per cent	SOY BEAN Per cent
Outdoors	103	95	60
Visible-spectrum	115	98	149
Full-spectrum	100	100	100
Blue	53	25	82
Minus-violet	103	97	141
Red	120	46	168
Shade	83	65	100

In considering the thickness of leaves, the extremes fall in the outdoors plants, where the leaves are thickest, and in the red house, where they are least thick. In two of the three forms measured (soy bean and four-o'clock), those growing in the full-spectrum house rank highest among the houses, that is, most nearly approaching outdoors plants; while the visible-spectrum plants made a close second. In the case of sunflower, the relation in these two houses is

just reversed. The minus-violet and shade leaves tally with each other very well, and the blue-house leaves, with their small size, prove but little different from these. The order here is (from the thickest to least thick): full-spectrum, visible-spectrum, blue, minus-violet and shade, and red-houses. The shade and minus-violet sunflowers are aberrant.

Here it is obvious that quality of light is effective in reducing the thickness of the red-house leaves, since the intensity (table I) is intermediate between that of the blue house and the minus-violet house, both of which have thicker leaves.

TABLE V

THICKNESS OF LEAF

HOUSE	FOUR-O'CLOCK Per cent	SUNFLOWER Per cent	SOY BEAN Per cent
Outdoors	110	154	133
Visible-spectrum	84	107	80
Full-spectrum	100	100	100
Blue	68	79	77
Minus-violet	66	100	66
Red	48	79	63
Shade	66	102	66

In studying the differentiation of the leaves, one finds that in sunflower and soy bean two layers of palisade cells ordinarily develop in outdoors conditions (fig. 1). In this feature, the full-spectrum leaves resemble those outdoors very definitely; while in the visible-spectrum house, lacking the ultra-violet rays, the second layer is weaker in soy bean. In all the other houses there is reduction to one layer, and in shade, with ultra-violet rays available, although in low intensity, we again find a vague second layer produced.

In four-o'clock (fig. 1) the long compact palisade layer, seen in outdoors leaves and in full and visible-spectrum leaves, does not develop in the other houses. In the shade house it is of intermediate length, while the cells in the minus-violet house are even shorter; in the blue house they are very open; and in the red, very short. In all cases leaves in the blue and red houses show a markedly poorer development than those in full or visible-spectrum houses. The weakest differentiation occurs in the red house.

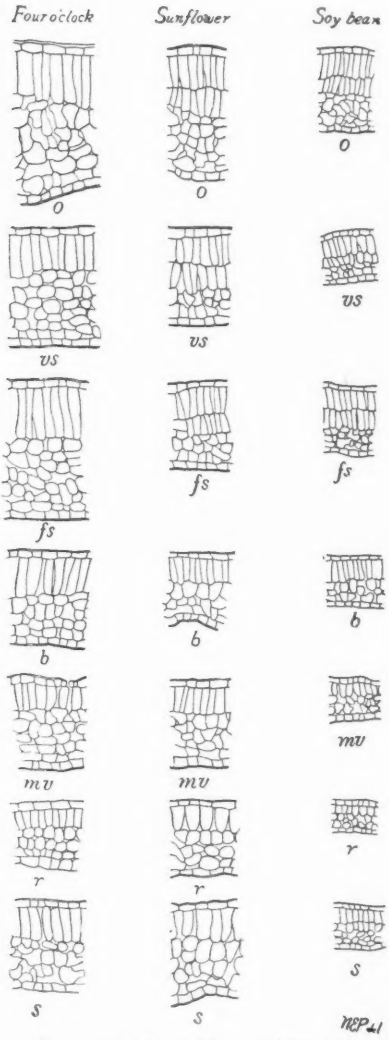

FIG. 1.—Sections of leaves of four-o'clock, sunflower, and soy bean from plants grown in different houses; houses are indicated by the following letters: *o*, outdoors; *vs*, visible-spectrum house; *fs*, full-spectrum house; *b*, blue house; *mv*, minus-violet house; *r*, red house; *s*, shade.

ROOTS.—It seems worth while to consider roots, but so far the material available renders it difficult to make any statement based on measurements, such as were made of the other organs. One may make an estimate on the basis of length, thickness, and development of secondary roots. Using this method, it was found that the outdoors plant takes precedence over any of the glass-house plants. Of the latter, the full-spectrum plant ranks first, the visible-spectrum next, the minus-violet plant (to which shade plants are similar) third, with the plants in the blue and red houses decidedly poor and feeble in comparison.

Discussion

It is difficult to make valid comparisons of plants in different situations where more than one factor varies. Hence the first two houses, which have approximately equal intensities, are the best ones on which to base conclusions as to the effect of quality of light. It seems evident that the plant in the full-spectrum house makes a better growth, so

far as differentiated tissues (as shown in vascular tissues in stem, diameter of stem, and thickness of leaf) are concerned; and it produced the usual form of plant, with the tissues commonly found in full insolation. The plant in the visible-spectrum house is weaker in vascular development, more spindly as to stem, with greater height, less thick as to leaf, and with poorer root development. The difference in light, that is, lack of most of the ultra-violet rays, results in this less stocky, less sturdy, more watery plant.

The same effect on form is noticeable in the two houses which emphasize the red end of the spectrum. Here, however, different

TABLE VI

SUMMARY: DEGREE OF DEVELOPMENT LISTED IN ORDER WITH THE HIGHEST FIRST

STEM			LEAF		ROOT
Vascular development	Diameter	Height	Thickness	Differentiation	Development
Outdoors	Full-spectrum	Visible-spectrum	Outdoors	Outdoors	Outdoors
Full-spectrum	Outdoors	Full-spectrum	Full-spectrum	Full-spectrum	Full-spectrum
Visible-spectrum	Visible-spectrum	Minus-violet	Visible-spectrum	Visible-spectrum	Visible-spectrum
Minus-violet	Minus-violet	Outdoors	Blue	Shade	Minus-violet
Shade	Shade	Blue	Minus-violet*	Blue	Shade
Blue or red	Blue or red	Red and shade vary in position	Shade*	Minus-violet	Blue
Red or blue	Red or blue		Red	Red	Red

* Exception in sunflower.

intensities, that is, lower ones, enter in as a factor, and may be partly responsible for the very weak stems, for the poor differentiation and thinness of leaf, and for the slight development of root.

It is unfortunate that in the blue house it has not been possible to obtain an intensity more nearly comparable with that of the full-spectrum house. At present it is impossible to dissociate the effects of quality and intensity of light in this house. In form the plants appear like miniatures of full-spectrum plants. Microscopic examination, however, shows very much weaker differentiation and development of tissue in stem and leaf. Whether the amount of food is the real limiting factor, that is, an indirect effect of light, or whether the light itself directly determines this, is not known.

Summary

Some sort of diagram, which would bring all these organs and their development into one view, seems a useful sort of summary.

Table VI serves this end. Usually outdoors plants take the first place, with the full-spectrum plants usually second, and visible-spectrum plants third. Except in height, which is the least tractable of the figures to handle, minus-violet-house and shade plants usually fall close together, and the blue- and red-house plants are generally at the end of the series, showing weaker development and differentiation. In the full-spectrum and visible-spectrum houses quality of light determines the difference, since the intensities are similar. In the remaining houses, both quality and intensity may be effective in bringing about the changes.

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EXPLANATION OF PLATES XV–XVIII

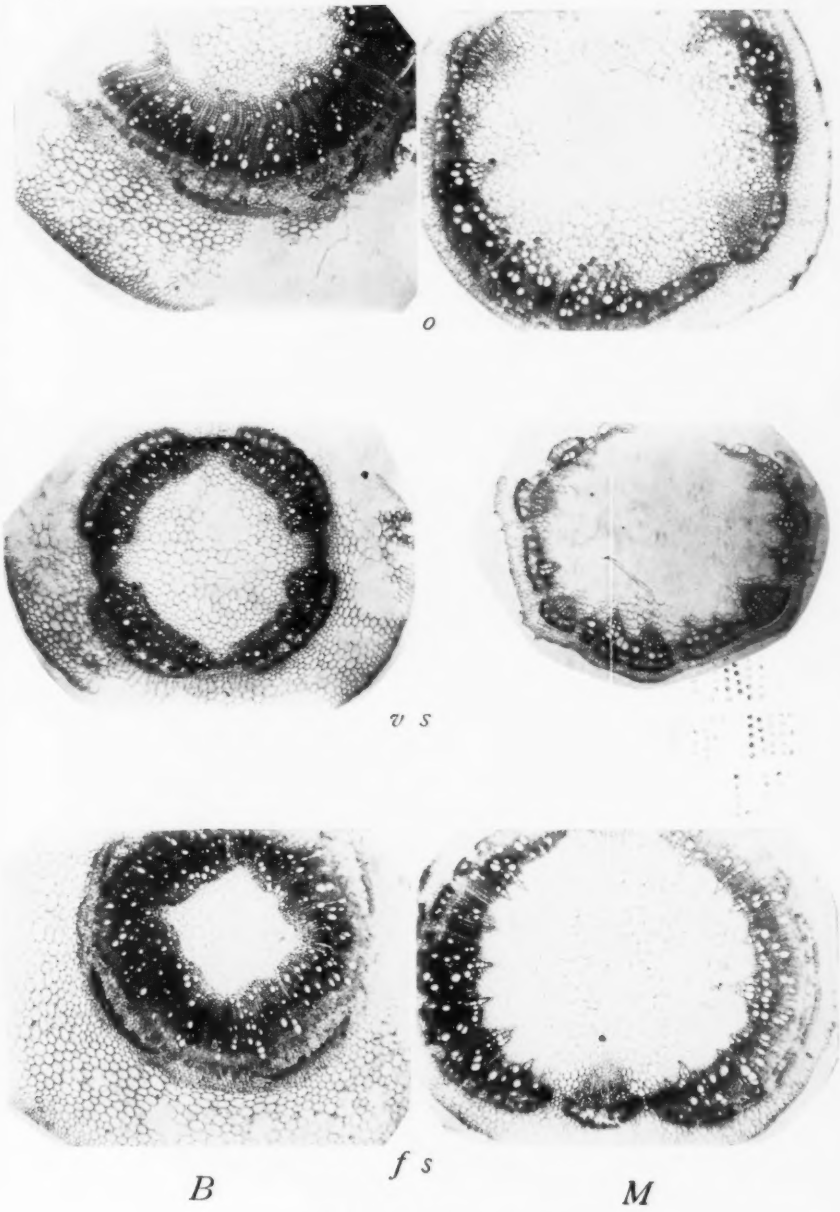
All photomicrographs of free-hand sections of stems were made with the use of the Leitz Makam micro-camera. In all plates the first column, *B*, shows the base of stem; the second, *M*, shows the middle of stem, half-way between base and apex. The smaller letters indicate locations in which the plants were grown: *o*, outdoors; *vs*, visible-spectrum house; *fs*, full-spectrum house; *b*, blue house; *mv*, minus-violet house; *r*, red house; *s*, shade. Plants were 14 weeks old.

PLATES XV, XVI

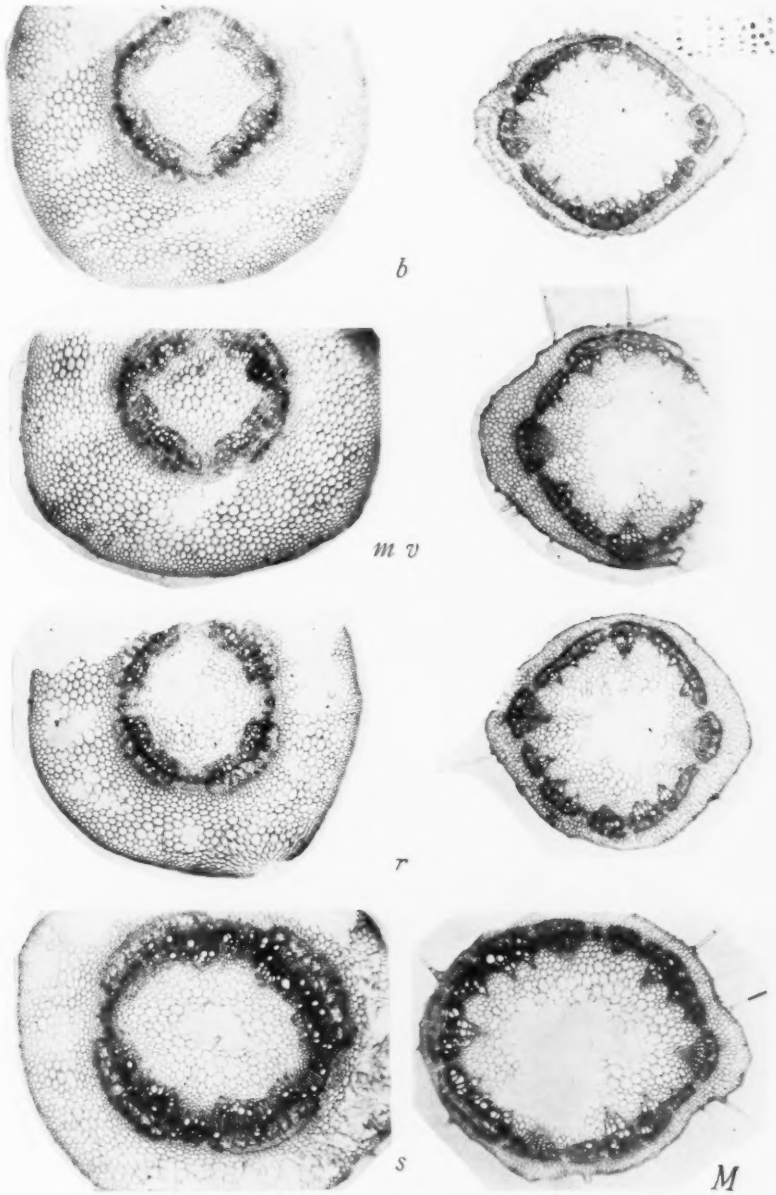
Glycine soja var. *biloxi*.

PLATES XVII, XVIII

Helianthus cucumerifolius, type of Henderson.



PFEIFFER on PLANTS AND LIGHT



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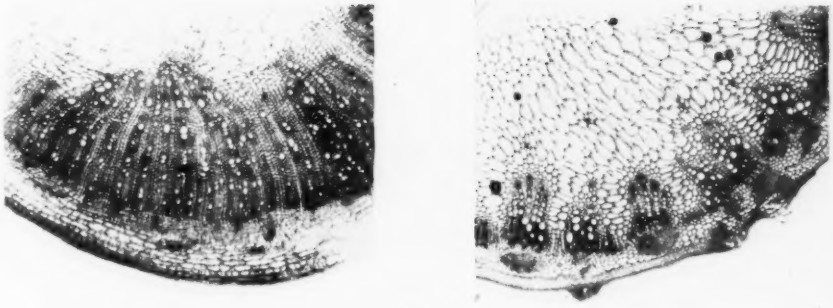
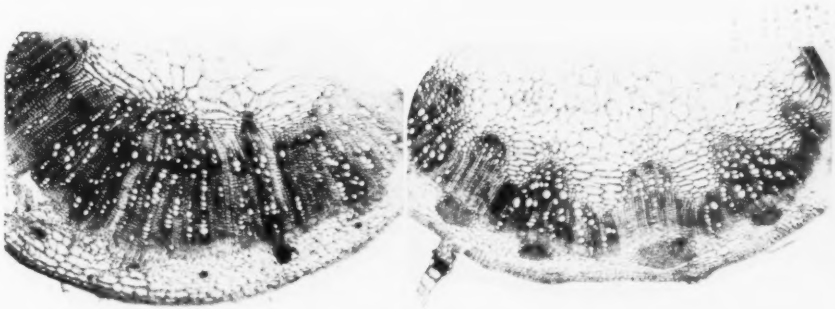


o



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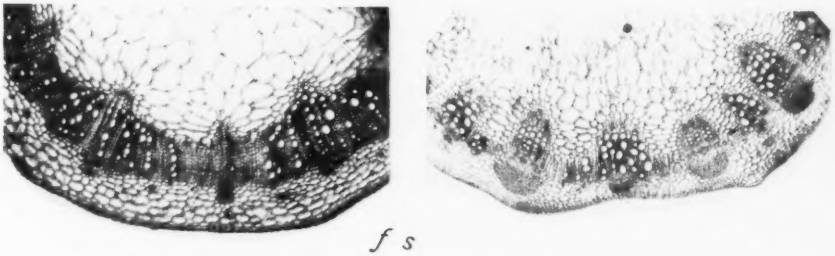

f s

B *M*

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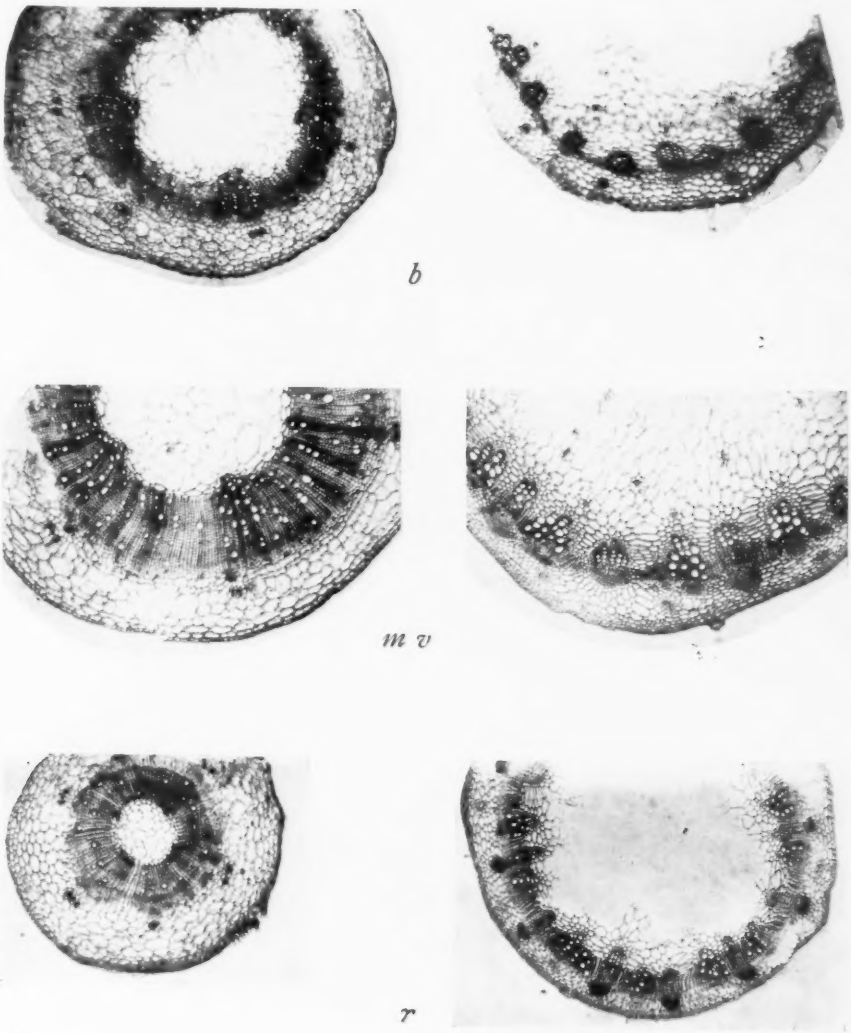

PFEIFFER on PLANTS AND LIGHT

MALE GAMETOPHYTE OF MICROCYCAS CALOCOMA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 381

DOROTHY G. DOWNIE

(WITH PLATES XIX–XXI AND ONE FIGURE)

Introduction

In 1907 CALDWELL and BAKER (2) published a taxonomic account of *Microcycas calocoma*, and a few months later the first author discussed its distribution in the field and described it morphologically (1). CALDWELL made no attempt to trace the development of either male or female gametophyte, as his material was inadequate; but he made the remarkable discovery of the occurrence of large numbers of sperms in the pollen tube, and correlated this with the increased development of archegonia in the female gametophyte. Since these publications, material has accumulated in this laboratory from collections made in the western Sierras of Cuba by CALDWELL in 1909, 1910, and 1911, covering a period from November 21 to April 24; by CHAMBERLAIN in September 1922; and by the writer in August and September, 1927. In 1924 MISS REYNOLDS (9) published an article on the development of the female gametophyte of *Microcycas calocoma*, and in 1926 Professor CHAMBERLAIN suggested to the writer that the development of the male gametophyte offered a fruitful field for further study.

The occurrence of many sperms in an antheridium is a feature of bryophytes and pteridophytes, in contrast with the two-sperm or male cell condition in the much reduced male gametophyte of the spermatophytes. Thus the development of the pollen grain in *Microcycas calocoma* might be expected to throw some light on the transition from the antheridium of the pteridophytes to the pollen tube of the seed plants. This study was undertaken, therefore, with a view to tracing the development of the male gametophyte and comparing it with that of other Cycadaceae, and also with the antheridial development of the leptosporangiate ferns. Progress in the bryophytic and pteridophytic antheridia is toward a gradual reduc-

tion in the primary spermatogenous cells, and in the output of spores. In the pteridophytes this is correlated with a reduction in the prothallial tissue. It was important, therefore, to demonstrate the number of primary spermatogenous cells, the generation of the sperm mother cell with reference to this, and the extent of the prothallial tissue. A brief examination of the pollen tubes indicated favorable material for the study of the blepharoplast, and it was hoped that in the division of the spermatogenous tissue the presence or absence of centrosomes could be established.

POLLINATION.—Field studies in Cuba show that pollination takes place during the last week of August and the first two weeks of September. By August 28 many male cones were shedding pollen and the female cones showed open cone scales. Examination of the ovules at this time, however, showed no development of the pollen chamber. By the second week in September the pollen chamber had appeared as a narrow vertical slit at the tip of the nucellus, and contained many pollen grains. As in other cycads, the pollen is shed in the three-celled condition, one prothallial, one generative, and one tube cell.

POLLEN TUBE.—The number of germinating pollen grains in one ovule is decidedly variable. While in general there are only one or two, as many as twenty-two have been counted in a pollen chamber. The exine of the pollen grain is almost uniform, tapering slightly to the point of exit of the intine, and it is very faintly etched with short parallel markings. The intine which grows out to form the pollen tube is thin at the grain end, but thickens and widens considerably just beyond the exine. It remains an almost uniform thickness for the rest of its length, and is irregularly lamellate. The pollen tube in its course penetrates the cells of the nucellus and absorbs their contents. This penetration is effected by a mucilaginous substance which arises from a transformation of the tube wall (figs. 9, 10). Occasionally the mucilage is found within the tube between the cytoplasm and the intine, suggesting that the substance may be, in part, secreted by the cytoplasm of the tube (fig. 11). The mucilage lies close to the cell wall of the adjacent nucellar cell, and appears to dissolve the cellulose of the wall, so that it becomes perforated and reacts differently to stain (fig. 8). Later notches appear (fig. 9),

which increase in size until the wall is penetrated. The solution is probably effected by enzyme action, but so far no tests have been made to determine the nature of the enzyme or the mucilage. The tube may attack the whole length of the wall at once, but more often its efforts are concentrated on a limited area, and once this is weakened sufficiently, the pressure of the tube bursts the wall (fig. 12). A protuberance then grows into the cell, gradually invading and finally filling it completely. Most of the cell contents are absorbed, but along the wall of the cell there collects a residue of undigested material, which takes up the iron-haematoxylin stain very deeply. This residue apparently acts as a barrier to the absorbing action of the mucilaginous intine, as the progress of the tube is often diverted. An area just behind the advancing point then secretes mucilage, and another cell is attacked in the same manner. The progress of the tube is thus slightly irregular, and this irregularity is enhanced or decreased according to the course of the tube. Generally the tube travels under the epidermis, one, two, or three layers deep in the tissue. The cells of the nucellus are elongate in this region, and a tube following the long axes of the cells meets comparatively little resistance. The result is a tube of fairly uniform diameter, with few or no protuberances or branches and only one effective point of advance (fig. 1). Occasionally a tube takes a more direct course toward the female gametophyte, that is, through the center of the nucellus. Here it meets isodiametric cells, which present a greater number of intervening cross walls per unit length traversed, and the tube is thus evolved into a wide irregular structure with several effective advancing points.

The tube nucleus occupies a position just behind the haustorial end of the tube, about 0.1 mm. distant in older tubes. It has a large nucleolus, surrounded at first by a dense chromatin network, which later becomes very loose and reacts rather faintly to the iron-haematoxylin stain. The nucleus finally becomes irregular in shape and often distinctly lobed. The cytoplasm of the tube is highly vacuolate. The vacuoles are large, and in the interstices collections of small granules, which stain deeply, often occur. In the youngest material starch is prevalent throughout the tube (fig. 3). Later it becomes scarce in the region of the body cells (figs. 5–8), but re-

mains abundant just behind the actively invading zone of the tube (fig. 12). When tube invasion of the nucellus ceases, and the tube nucleus passes back to the body cell region, starch accumulates at the grain end again, occurring as large spherical granules densely aggregated in the tube and in the prothallial and spermatogenous cells (fig. 18). At this time the free end of the tube is much swollen and the intine is stretched and thin, while the body cells are actively dividing. On the division of the body cells and the formation of the sperms the tube ruptures and the sperms escape into the pollen chamber.

PROTHALLIAL CELL.—At pollination, and during the early development of the tube, the prothallial cell has a dense cytoplasm and a well defined nucleus (figs. 2–4). Later the cytoplasm becomes diffuse, owing to the formation of large vacuoles; and the nucleus, although large, stains deeply with iron-haematoxylin, almost suggesting disorganization (figs. 7, 8). A tube stained for the study of the body cells is too deeply stained for critical examination of the prothallial and stalk cells. The nucleus of the prothallial cell sometimes shows a slight activity, entering into a late prophase stage (figs. 6, 13). This activity is manifest between successive divisions of the spermatogenous cell, but no division takes place.

By December the prothallial cell has increased considerably in size and has grown well into the stalk cell (figs. 14–17). The cytoplasm has become denser and the nucleus stains normally. What at first was a common dividing wall between stalk and prothallial cells has now split into two distinct walls, which remain in close juxtaposition (figs. 13, 14). While in all other Cycadaceae, where this phenomenon has been described, the prothallial cell grows until it presses against the farthest wall of the stalk cell, in *Microcycas* it does not halt there, but grows right through the wall as a long narrow papilla extending among the body cells (figs. 15–17). This passage of the prothallial protuberance through the stalk is not accompanied by any violent rupture of the latter. The stalk cell remains turgid and appears as a closely investing funnel cell. It would appear that the prothallial cell carries forward with it the basal wall of the stalk cell, until the opposing walls of the latter meet and fuse. Further growth of the prothallial cell then ruptures the fused

wall, without disturbing the cytoplasmic contents of the funnel-shaped stalk cell. The protruding papilla grows until it is almost equal in length to the normal part of the cell. It increases also in width, and finally expands so much that it bulges over the stalk cell. The nucleus always remains in the lower part of the cell, and is surrounded by a highly vacuolated cytoplasm, in which numerous spherical starch grains are imbedded (fig. 18).

The renewed activity of the prothallial cell seems correlated with a period of quiescence in the stalk cell. This situation will be discussed further, therefore, at the close of the description of the stalk cell.

GENERATIVE CELL.—At pollination the generative cell resembles the prothallial cell in appearance, and is separated from it by a common wall (figs. 2, 3). Later it increases in size and appears to fit like a cap over the lenticular prothallial cell. After enlarging, it divides to give rise to a body cell and the stalk cell (fig. 4).

STALK CELL.—The stalk cell has a characteristic shape, and practically fills the tube at the grain end, but does not extend beyond the narrow zone inclosed by the exine in the September-October material. The cytoplasm of the cell is fairly dense, and contains a few scattered granules which stain deeply. The nucleus is large and slightly excentric in the cell, and the nucleolus is surrounded by a large hyaline area (fig. 6).

The name "stalk cell" was originally given to this cell because it was thought to be the same morphological unit as the stalk cell in the antheridium of the bryophytes and the pteridophytes. This cell is sterile throughout the gymnosperm phylum, with very few exceptions; and this fact, together with its position between the prothallial and the fertile spermatogenous or body cell, gave rise to this conception. Within recent years doubt has been placed on this analogy, but nevertheless the name has been retained in the literature. The writer's findings in *Microcycas calocoma* refute this analogy entirely, and prove, I believe, that the stalk cell is a sterile spermatogenous cell; for in this species the so-called stalk cell is an actively dividing cell, capable of as many as ten or eleven divisions, and cutting off at each division a body cell (figs. 5, 7, 8). This activity takes place during the months of September and October, and follows immedi-

ately the division of the generative cell. I would therefore regard the generative cell as a primary spermatogenous cell, comparable to the cell so named in the lower groups, and the stalk cell as a spermatogenous cell active in *Microcycas calocoma*, but having lost the division potentiality in the other gymnosperms. Such a loss is foreshadowed in *Microcycas calocoma*, where the number of body cells varies from eleven to eight. It should be noticed that the successive divisions of the stalk or spermatogenous cell take place in the same plane, and that a linear arrangement of the body cells in basipetal succession is thus formed.

One interesting exception to this linear arrangement of body cells of increasing age and size was encountered. In this case there appeared two spermatogenous cells in the following order: prothallial cell, spermatogenous cell (1), body cell (1), spermatogenous cell (2), body cell (2), body cell (3), (text fig. 1). Body cell (2) was obviously derived from spermatogenous cell (2), while body cell (3) might have been derived from either spermatogenous cells (1) or (2), although more probably from (2). It would appear that, on the division of the primary spermatogenous or generative cell, both daughter cells had retained the power of division, or that the daughter cell of the second division had retained this potentiality. No other tube has been found showing this variation. It may be that this exception is of historical significance, pointing to a loss in the division potentiality of the daughter cells, the body cells, suggesting at one time an even greater number of spermatogenous cells and a correspondingly larger number of sperms.

The demonstration of centrosomes in the spermatogenous cells of *Marsilia* (10) suggested the possibility of this structure appearing in *Microcycas calocoma* during the division of the "stalk" cell. A careful study of this cell in division and in the resting stage failed to reveal such a body. The rounded end of the spindle might help to confirm the absence of centrosomes.

About the end of October the spermatogenous cell becomes sterile, and it enlarges and grows out of the grain end of the tube. The prothallial cell has also started to grow, and in pushing its way through the covering cell, it displaces the nucleus of the spermatogenous cell to one side. The manner of the subsequent growth of

both these cells has already been discussed. Although enlarging greatly, the "stalk" cell fails to keep pace with the prothallial cell. Both cells at this time are packed full of starch. The further history of these two cells could not be determined, but in all probability, coincident with the bursting of the tube they also burst and discharge their contents.

As an explanation of the occurrence of the body cells in a basipetal series (figs. 6–8), Professor LAND put forward the following suggestions. First, the linear arrangement of the body cells is due to the configuration of the tube, and second, the activity of the spermatogenous cell is dependent on the course of the food stream. He is under the impression that in some way nutrition is inhibited from entering the spermatogenous cell directly, and that therefore it receives its supply by way of the prothallial cell. Always the daughter cell in juxtaposition to the prothallial cell obtains a greater supply of nourishment, and its growth is therefore more rapid than the other daughter cell (fig. 5). In contrast to the slow growth of the body cells, there is a rapid development of the stalk or spermatogenous cell, so that it is soon stimulated to divide again. The absence of starch at the grain end of the tube in the early stages made it impossible to test out the second part of this theory, but I think the phenomenal development of the prothallial cell, in the later stages of its history, almost establishes this explanation as a fact. For as long as the spermatogenous cell was actively dividing it made great demands on the prothallial cell, but once the former entered into a period of comparative quiescence, the latter, still receiving large supplies, was enabled to grow rapidly. Both obtain unlimited food supply, as shown by their starch content; but the prothallial cell exhibits the more phenomenal increase, easily surpassing its neighbor. This would appear the normal sequence of events if the food stream entered the spermatogenous cell by way of the prothallial cell.

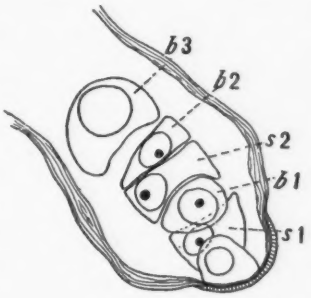

FIG. 1

BODY CELL.—Owing to the oblique spindle of the spermatogenous cell in division, the body cell is at first wedge-shaped in longitudinal section. The nucleus is large, excentric, occupying the broad end of the wedge, and extending the full width of the cell in one direction. The cytoplasm is fairly dense, the vacuoles small, and granules that stain black with iron-haematoxylin are scattered through the cytoplasm or grouped at the interstices between the vacuoles. Starch is absent. Two blepharoplasts soon appear in the cytoplasm of the body cell at opposite poles (figs. 6, 7).

The body cell and its nucleus increase greatly in size, the cell becoming first oblong, and then rounded on the side away from the grain. Finally it becomes completely spherical, and remains so during the rest of its development, only continuing to increase in size. The nucleus and the blepharoplasts enlarge considerably. In the tube a regular series of body cells is present, from the youngest, next the spermatogenous cell, to the oldest at the tube end (figs. 6–8). Only one linear row is found, emphasizing the fact that the spermatogenous cell divides always in one plane. Several months later, just before the formation of the sperm mother cells, this serial arrangement is lost. The tube widens at the free end, and the spherical body cells, alike in size and structure, are scattered or grouped in a mass. Apparently growth in the younger body cells is more rapid than in the older, so that a universal developmental stage is reached just before division. The rapid enlargement of the spherical body cells in the limited confines of the tube thus causes a displacement of the linear row. The intine is stretched, and is seen to inclose a mass of similar cells which divide almost simultaneously to form sperm mother cells.

BLEPHAROPLAST.—The cytoplasm of the young body cell, just after it has been cut off from the spermatogenous cell, is uniform. Soon small granules appear which stain black with iron-haematoxylin. They are scattered in the cytoplasm, and appear to have no relationship to the nucleus. Later they collect in groups (fig. 20), and a definite blepharoplast suddenly appears. As first observed, it seems to be composed of a tiny aggregate of these black granules (figs. 19, 21). The small granules fuse into larger ones, and into a uniform mass which becomes conspicuous in the cell (fig. 22). The

aggregate of small granules appears to be an attractive center, as there soon arise granular stream lines flowing into it on all sides. It appeared that the blepharoplast was formed by the flowing together of these small granules which arise in the cytoplasm. There may be a few small aggregates, but one takes precedence and acts as a center for the stream lines of granular material. One blepharoplast appears well in advance of the other. Often two new body cells have been cut off by the spermatogenous cell before a body cell has both its blepharoplasts. The second blepharoplast arises in the same way but on the opposite side of the cell. Always they appear in the cytoplasm and at some distance from the nucleus. Although the stream lines are distinct in themselves, the cytoplasm in the neighborhood suggests a wavelike zonation, surrounding a narrow hyaline area in immediate contact with the blepharoplast (figs. 17, 23).

After the fusion of the granules, the blepharoplast remains a uniformly staining body for some time. Later the central area does not take the stain so deeply, but the margin remains dense. The stream lines have elongated considerably, and the zonation of the cytoplasm is still manifest. The blepharoplast has gradually approached the nucleus. At first the latter appears to beak slightly toward it (fig. 21); later the nuclear membrane becomes concave and the blepharoplast appears to lie in this hollow (fig. 23). Just before the division of the body cell the conditions are reversed. The nucleus is still hour-glass shaped, but the blepharoplasts occupy the farthest poles of the cell. The body cell is now quite spherical, but the blepharoplasts are flattened plates and are highly vacuolate (fig. 24). They occupy the opposite poles, and from them strong stream lines radiate. The vacuolated plate then seems to disorganize. Pieces are broken off which scatter in the cytoplasm (fig. 25). Each of these pieces seems to elongate and to develop protrusions, which at first are large and irregular, and then become ciliate (fig. 26). CALDWELL describes the blepharoplast as first giving rise to a distinct band which later may break up into fragments. This is not in accordance with my findings. Unfortunately the material at this stage was limited, and I was unable to decide whether the breaking up of the blepharoplast was a sign of the disorganization of the body cell, or the beginning of the formation of the ciliated band of the sperms.

The development varies considerably from the description of such stages in *Dioon* (3), *Stangeria* (5), *Ceratozamia* (4), and *Bowenia* (7).

Material for a more complete study of the transition from blepharoplast to ciliated band will be available when the cones, artificially pollinated by the writer in September 1927, are received in this laboratory.

SPERM MOTHER CELL AND SPERM.—CALDWELL has described briefly the mature body cell and the formation of the sperm. As only isolated stages of this later development are available, the present paper cannot add anything to this description.

Discussion

The generative cell throughout the spermatophytes appears to be synonymous with the primary spermatogenous cell of the pteridophytes. Its product, the stalk cell, while sterile in all genera, is fertile in *Microcycas;* and it is probable that the four-sperm condition noted in *Ceratozamia* (4) may have resulted from the division of this cell. Further evidence of this potential fertility is produced by the situation in *Phyllocladus* (12) and *Dacrydium* (11). Here the generative cell divides into two collateral cells. In general one develops more rapidly than the other, resulting in a fertile body cell and a sterile stalk cell; but it has been recorded that both cells may develop into fertile body cells.

However, that all cases cited in the gymnosperms, where more than two male cells occur, are due to a revival of this latent activity of the stalk cell is very debatable. The stalk cell, and perhaps the body cell also, began its history as an active spermatogenous cell. An evolutionary tendency to a reduction in the number of archegonia in the female gametophyte, and of sperms or male cells in the male gametophyte, produced a gradual decrease in the activity of the spermatogenous cell, and it ultimately became sterile. This latter condition has been reached by all the living gymnosperms except *Microcycas*. In the Cupressineae, however, there is a reversion toward an increased number of archegonia inclosed in a common jacket, and a correlated increase in the number of male cells is therefore not unexpected. This situation has actually arisen in *Cupressus goveniana* (6) and *Juniperus communis* (8). By this time, however, the stalk cell is not only sterile but degenerate, as in many Cu-

pressineae no definite cell is organized. The increased activity is assumed by the body cell, therefore, and the large output of male cells is the result of the division of this cell. These cases are exceptional, however, and the evidence at present is so scanty that this explanation must be accepted as mere speculation.

One-half of this first generation of the primary spermatogenous or generative cell having become definitely sterile, it is not remarkable to find in the angiosperms a complete elimination of a generation of spermatogenous tissue, and the generative cell dividing directly to form male cells.

The linear arrangement of the body cells is concomitant with the configuration of the tube, and the latter is a condition resulting from the seed habit. The evidence of a transition from a spherical mass of spermatogenous tissue, such as we find in the antheridia of bryophytes and pteridophytes, to a linear arrangement of cells, as in *Microcycas calocoma* pollen tubes, could only be traced in ancient seed plants. Seeds of the Carboniferous era, where the male gametophyte has been at all preserved, suggest a spherical body with a comparatively large development of spermatogenous tissue. Just why the tube arose is a subject for speculation at present, but it carried in its wake a gradual elimination of spermatogenous cell divisions, except in one plane, and this gave rise to the uniseriate arrangement characteristic of the gymnosperms today.

The rise of the pollen tube is perhaps correlated with an increased separation in time of pollination and fertilization. In early forms the male gametophyte was probably shed from the microsporangium at complete maturity. The seed with its well developed pollen chamber received the microspore with its mature sperms, and the latter came to lie almost directly on the necks of the archegonia. An earlier shedding of the pollen would necessitate the further development of the male gametophyte taking place in the seed. To obtain nourishment the microspore developed a haustorium. Correlated with this early shedding of the microspore is an insufficiently developed pollen chamber, so that a tissue intervenes between pollen grain and archegonia. If the grain continues to be shed earlier and earlier in the life history of both gametophytes, a condition would arise comparable with that of the living gymnosperms.

Summary

1. Pollination appears to take place during the last week in August and the first two weeks in September.

2. The pollen is shed in the three-celled condition, one prothallial cell, a generative cell, and a tube cell.

3. The generative cell divides, giving rise to a "stalk" cell and a body cell. The stalk cell is a fertile spermatogenous cell undergoing eight to ten successive divisions, each time cutting off a body cell. Centrosomes were at no time present in the spermatogenous cell.

4. The body cells divide once only, producing two-sperm mother cells. One exceptional case is described where a daughter cell, which normally would have become a body cell, remains spermatogenous.

5. The pollen tube moves through the nucellar tissue by solution of the cell walls and absorption of the cell contents.

6. There is only one prothallial cell.

7. The prothallial cell remains small until cessation of the activity of the spermatogenous cell. It then grows rapidly into and through the stalk or spermatogenous cell.

8. The spermatogenous cell remains turgid during the passage of the prothallial cell.

9. The blepharoplast appears in the young body cells as an aggregate of small granules.

10. After the enlargement and vacuolation of the blepharoplast, pieces are broken off which scatter in the cytoplasm of the sperm mother cell. This may be a process of disintegration.

11. Owing to insufficient material, the formation of the ciliated band could not be determined. A further study of this phase will be reported in a later paper.

12. The number of sperms ranges from sixteen to twenty.

In conclusion, I wish to acknowledge my indebtedness to Professor C. J. CHAMBERLAIN for suggesting the problem, and for his continual encouragement throughout the work, and to Professor W. J. G. LAND for helpful discussion and suggestions. I should also like to thank Dr. R. M. SAN PEDRO of Consolacion del Sur and friends in Cuba for their helpfulness in the field and their kindness in forwarding material.

UNIVERSITY OF CHICAGO

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EXPLANATION OF PLATES XIX-XXI

PLATE XIX

FIG. 1.—Longitudinal section through integument, *int;* nucellus, *nu;* and pollen chamber, *pc*, showing reconstructed pollen tube (*t*), with its tube nucleus (*tn*); September; ×100.

FIG. 2.—Longitudinal section of pollen grain as found in pollen chamber, September 15; ×860.

FIG. 3.—Longitudinal section of pollen tube, tip of which has grown into nucellus, showing prothallial cell (*p*), generative cell (*g*), tube nucleus (*tn*); September 15; ×860.

FIG. 4.—Longitudinal section of pollen tube; generative cell divided into "stalk" cell and first body cell; prothallial cell (*p*), spermatogenous cell (*s*), and body cell (*b*); September 21; ×860.

FIG. 5.—Section of pollen tube showing prothallial cell, spermatogenous cell, and body cells; division of spermatogenous cell just completed; September; ×1580.

FIG. 6.—Section of grain end of tube showing prothallial cell, spermatogenous cell, and linear arrangement of body cells; September; ×1260.

FIG. 7.—Longitudinal section of pollen tube showing prothallial cell (*p*), spermatogenous cell (*s*), and body cells (*b*); nucleus of spermatogenous cell in prophase; September; ×1260.

FIG. 8.—Section of pollen tube showing prothallial cell (*p*), spermatogenous cell (*s*), and body cells (*b*); nucleus of spermatogenous cell in anaphase; September; ×1260.

FIG. 9.—Advancing point of pollen tube showing intine (*i*), mucilage (*m*), and undigested material (*u*); wall of nucellar cell in front of tube notched; ×2200.

FIG. 10.—Advancing point of pollen tube (*t*), showing partial absorption of nucellar cell wall (*w*), undigested material (*u*), intine of tube (*i*), and mucilage (*m*); ×2200.

FIG. 11.—Advancing point of pollen tube (*t*), with mucilage (*m*) between intine (*i*) and nucellar cell wall, and intine and cytoplasm of tube; ×1390.

FIG. 12.—Advancing point of pollen tube (*t*), intine (*i*), undigested material (*u*), and starch (*st*); nucellar cell wall ruptured and intine pressing into cell; ×1390.

PLATE XX

FIG. 13.—Enlarged view of tube illustrated in fig. 6, showing prothallial cell (*p*), spermatogenous cell (*s*), and body cell (*b*); nucleus of prothallial cell in early prophase; common wall between prothallial cell and spermatogenous cell split into two in part; ×2200.

FIG. 14.—Prothallial cell and spermatogenous cell showing split in common wall almost complete.

FIG. 15.—Section of pollen tube at grain end, showing prothallial cell (*p*), funnel-shaped spermatogenous cell (*s*), and body cell (*b*); prothallial cell has grown through spermatogenous cell, but latter still turgid; December; ×1260.

FIG. 16.—As in fig. 15: prothallial cell has developed long papilla; January; ×1460.

FIG. 17.—As in figs. 15 and 16: papilla of prothallial cell has increased in volume; cytoplasm seems to show zonation around blepharoplast; January; ×1460.

FIG. 18.—Later stage in development of prothallial cell and spermatogenous cell; both filled with starch; April; ×1260.

PLATE XXI

FIG. 19.—Body cell showing early stage in formation of blepharoplast; this cell is second youngest body cell of tube in fig. 6; September; ×2200.

FIG. 20.—Same body cell at slightly different depth; granules all collected in region of blepharoplast; September; ×2200.

FIG. 21.—Older body cell with blepharoplast showing as aggregate of granules (oldest body cell of tube in fig. 6); September; ×2200.

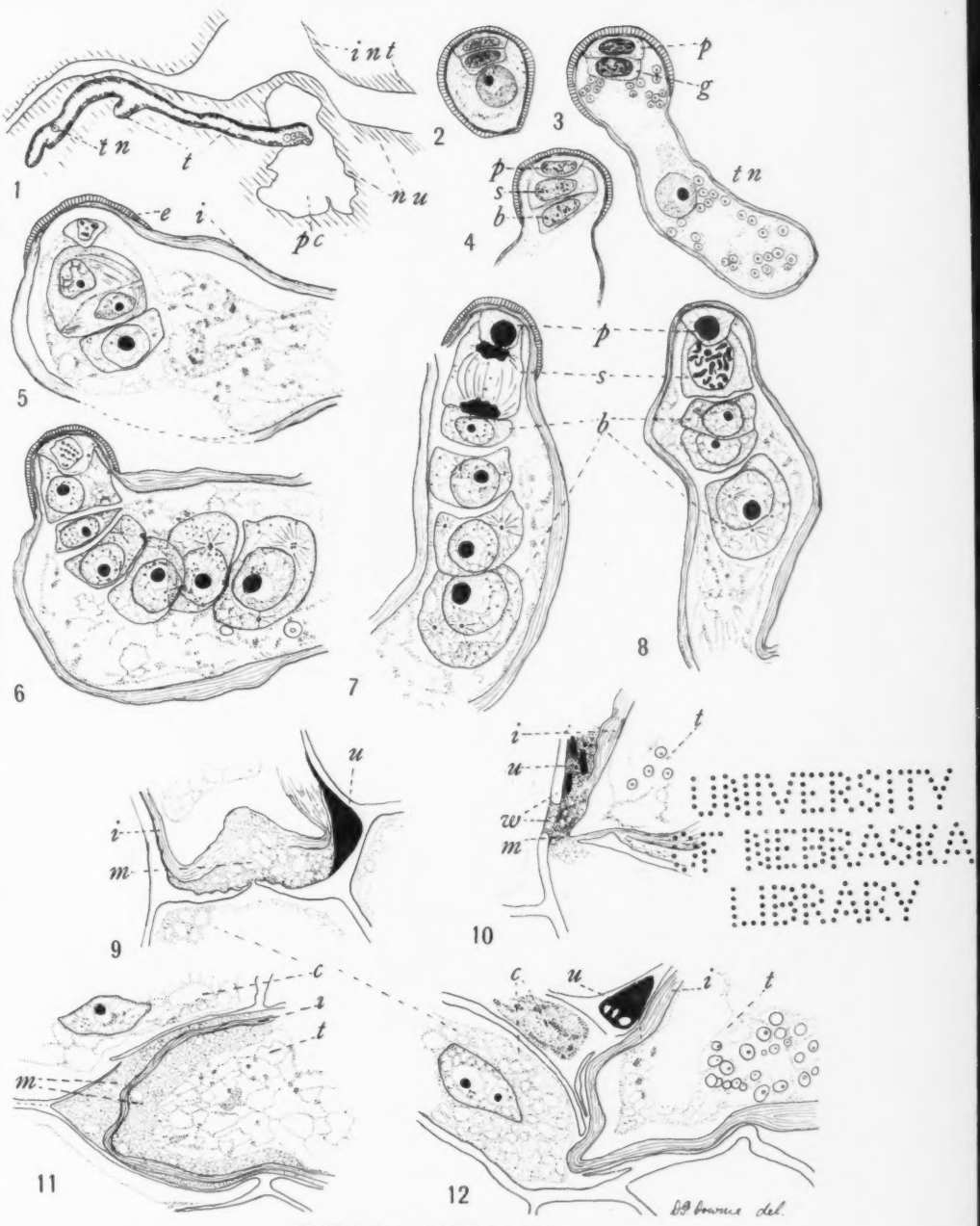
FIG. 22.—Blepharoplast now a uniformly staining body; December; ×2200.

FIG. 23.—Blepharoplast surrounded by zoned cytoplasm; January; ×2200.

FIG. 24.—Later stage in development of blepharoplast, showing vacuolation; February; ×2200.

FIG. 25.—Still later stage in development of blepharoplast; fragments shown broken off from central area; February; ×2200.

FIG. 26.—Scattered fragments have developed protuberances; in one case a bandlike projection is shown; February; ×2200.



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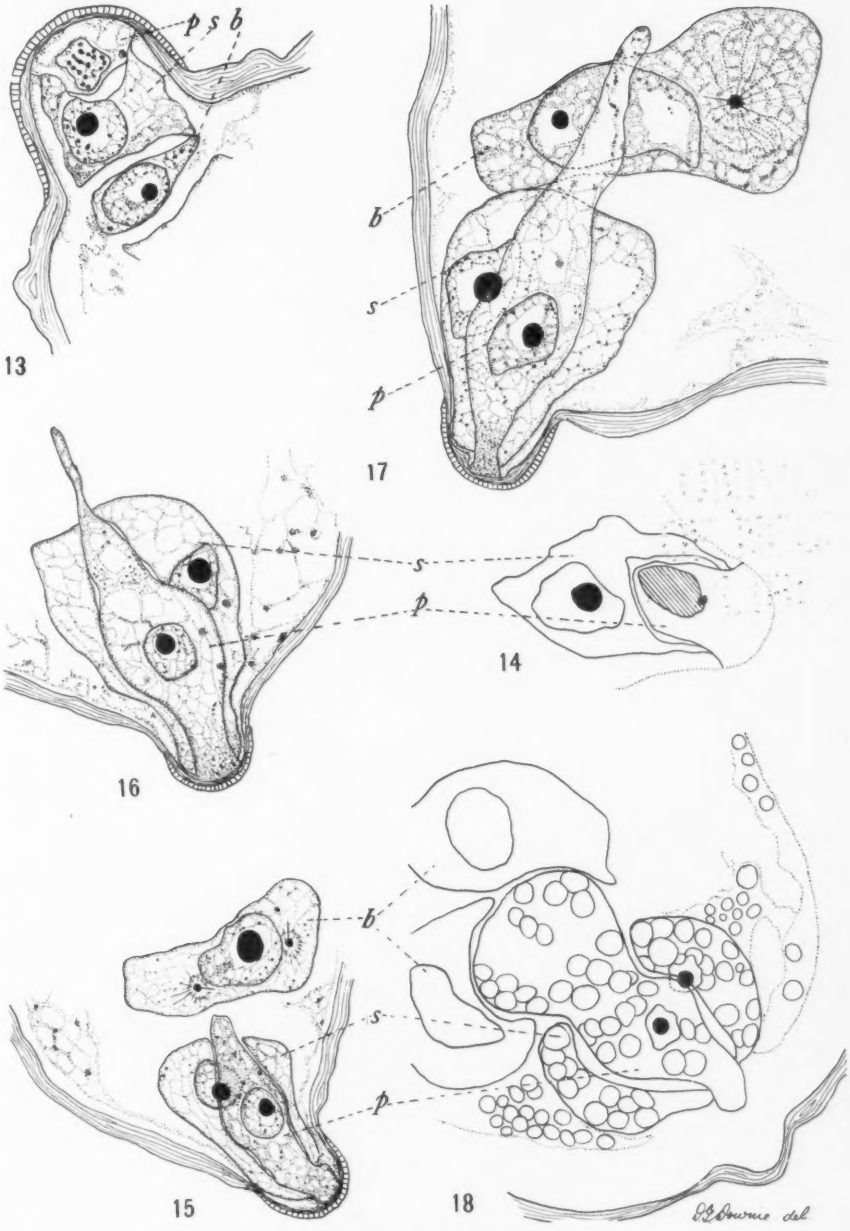

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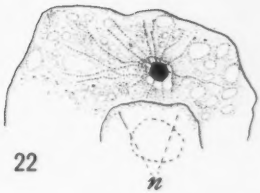

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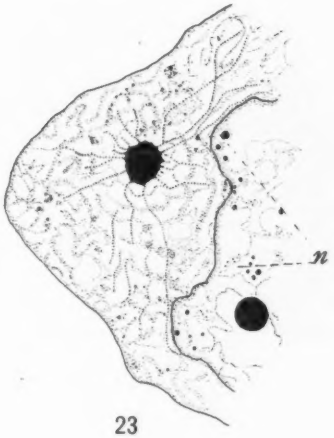

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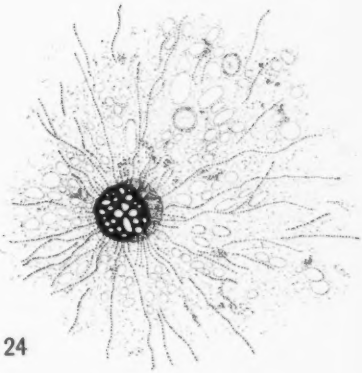

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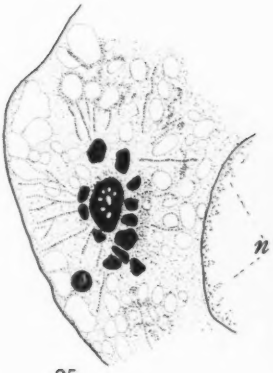

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NUTATION IN PINUS SYLVESTRIS[1]

FRANK C. GATES

(WITH FIVE FIGURES)

During 1923 at Manhattan, Kansas, some curious differences of positions were noted on different days among the elongating shoots of a *Pinus sylvestris* which was being observed daily. This led to a series of observations and measurements during the four subsequent springs. The following paper is based on these observations.

The differences in position of the elongating shoots from day to day were very striking. Continuous observation for a few days showed too great a factorial regularity to be chance nutation. The factorial possibilities quickly reduced the causal effect to two principal ones; namely, wind and sun, both of which acted through differentiation of the growth by influencing the turgidity, as is possible by differentiation of the water balance. The bends or curves occurred only during a time of growth and ceased as soon as the longitudinal axis completed its elongation. The same effect was often seen on *Pinus banksiana* and a few times on *P. strobus* (fig. 1) in northern Michigan, but no trees of these species were available for daily observation. Two other pines, *P. laricio* and *P. ponderosa*, which were convenient for continued daily observation, showed no trace of this bend. In both of these cases the elongating stem was very stout, greatly contrasting with the slender, more rapidly elongating stems of *P. sylvestris*.

A priori, one might expect to find these tender shoots being blown with the wind, and consequently it was somewhat surprising not to find this more than once during the whole series of observations. This time was when a very strong wind, over 45 miles an hour, had full access to the tree (fig. 2). Aside from this the shoots were curved into the wind (fig. 3). The apparent mechanism was simply that of increased water loss on the side toward the wind, resulting in a forcing over into the wind because of the greater water pressure and

[1] Contribution no. 279, Department of Botany and Plant Pathology, Kansas State Agricultural College.

growth on the opposite side. Apparently the effect of sun was similar; the differentiation of the temperature brought about differentiation of the transpiration, causing differentiation of the water pres-

FIGS. 1–3.—Fig. 1, *Pinus strobus* at Douglas Lake, Michigan, showing shoots curved into the setting sun (June 26, 1927); fig. 2, *P. sylvestris* with topmost leader flying with southeast gale; all other shoots had made the change from northwest (fig. 3) into southeast with the change of wind; a little later in the day the topmost leader likewise curved into the southeast (April 20, 1925); fig. 3, *P. sylvestris* earlier on the same day as fig. 2; all shoots bent into strong northwest wind.

sure, bringing about growth curves into the direction of the sun. The actual result depended upon which was stronger; usually a wind strong enough to rustle the leaves of ordinary trees was suf-

ficiently strong to cause a curve into the wind, irrespective of the sun; with the air hardly stirring, curves into the sun were most conspicuous somewhat early in the day and again late toward night, suggesting positive heliotropism.

While there was a certain amount of variation, usually all leaders of the main stem and branches acted alike, and usually the whorl of

FIGS. 4, 5.—Fig. 4, *Pinus sylvestris* in virtually no wind, showing bending of leaders into sun shortly after sunrise (April 12, 1925); fig. 5, *P. sylvestris* after a rainy night accompanied by a sharp northwest wind; picture taken shortly after wind died down and sun came out of clouds in east; the more prompt response of topmost leader is shown (May 4, 1926).

branches at the base of the leader responded similarly. Variations were most likely to occur when the factors were less strong, and particularly when parts of the plant aided in preventing the operation of a factor, as, for instance, the north side shaded from the sun. In general the leaders were more active (figs. 4, 5). One would expect this from the fact that the leaders elongate more rapidly and to a greater degree than do the whorls of branches. During cool spells

the amount of curving was checked and became more erratic, but also the amount of growth was greatly checked. Normally, rainy weather tended to increase the quantity of the response. In very light wind the extra water at first on one side would occasionally bring about responses away from the direction of the wind or rain, followed by irregular bends during the duration of the rain.

A few of the daily observations may be mentioned as samples.

1924

April 21, 7:00 A.M., 10° east into the sun, no wind; 3:30 P.M., 5° northwest into the wind and sun, the sun seemingly of stronger effect as the bend did not occur until afternoon.

April 22, 7:00 A.M., 22° northwest into wind opposite from sun.

April 24, 8:00 P.M., 30° east into wind away from the setting sun.

April 25, 7:00 A.M., upright, a cloudy windless morning.

April 28, 10:00 A.M., 10° east into sun, the plant really protected from a slight southwest wind; 8:00 P.M., followed sun across the sky and at sunset was 45° west; after sundown it straightened up to 7° west, no wind to speak of and that little did not strike the tree.

April 29, 7:00 A.M., following a light misty rain most of the late part of the night with a light easterly wind, leaders were bent to the west 10–20°, the curve being particularly conspicuous in growth region; 9:00 P.M., nearly erect at 6:00 P.M., but in the evening a 20° bend eastward into a gentle cool wind.

May 2, 6:00 A.M., mostly with a sharp 30° curve into the east to the sun, no wind; 8:00 P.M., after a light shower in the afternoon bent up to 40° into the sun at 5:40, but by 8:00 had straightened up to 10° northwest.

May 5, erect all day in strong southwest wind which did not hit the tree very sharply; toward night the wind died down and the leaders bent slightly to the setting sun; elongation now virtually completed, consequently bends less prominent.

1925

April 7, elongation reached 61 mm. at this date, but no bends had been as yet noticed.

April 8, 7:00 P.M., slight bends for the first time noticed toward the west into the wind and sun.

April 12, 8:00 A.M., elongation now beginning to be rapid; 10° east before sunrise into a very light wind, changing to a more prominent bend into the sun (fig. 4) and following the sun across the sky to a 10° west bend at 6:00 P.M., virtually no wind all day.

April 15, 7:00 A.M., erect, a cloudy day.

April 16, 7:00 A.M., east into wind and sun 20°; 7:00 P.M., west into sun 10° in spite of a light east wind.

April 17, 8:00 P.M., bends up to 25° east into a sharp breeze.

April 18, 6:00 P.M., after breeze during the day had died, the leaders erected and went over to as much as 30° northwest into the sun, although the light breeze remained southeast.

April 19, 8:00 A.M., a strong north wind during the night, and at daybreak leaders bent northwest into it in spite of the sun.

April 20, 1:30 P.M., a very strong northwest wind had had all the new growths bending into it as the sun came up (fig. 3), but when the wind changed to southeast and increased all morning to gale intensity, the growths were blown with it for about three hours, but at 1:30 only the uppermost leaders were with it (fig. 2), all others had curved 10–20° into this southeast wind; sun obscured much of the time; by 5:30 the uppermost leaders had finally curved into this southeast wind.

April 25, 7:00 A.M., upright in a fog.

April 26, 7:00 A.M., slightly northwest into a cool northwest wind; needles now developing rapidly and elongation of stem had ceased and no further bends were noticed.

Summary

1. A long series of observations on the elongating shoots of *Pinus sylvestris* showed that during the elongating period the new shoots are subject to nutations, which are caused by differentiation of the water pressure on the different sides, resulting in growth curves in the direction where the turgidity was least. The two agents that thus operated locally to decrease turgidity were direct sun and wind. In the absence of either, the shoots were erect.

2. The same effects take place regularly upon the slender-shooted *Pinus banksiana* and *P. strobus*, but were not present on the stout-shooted *P. laricio* and *P. ponderosa*. In general the wind seemed to have a greater effect than the sun, as long as it was strong enough to rustle leaves of ordinary trees. The effects were greatest when wind and sun operated together, but changes from one position to another following changes of the factors could be quite rapid.

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PHYSICAL AND CHEMICAL CHARACTERISTICS OF EXPRESSED CITRUS LEAF SAP AND THEIR SIGNIFICANCE[1]

A. R. C. HAAS AND F. F. HALMA

It has been shown by HAAS (1) that the ash and calcium of the water-soluble fraction of mature normal Washington Navel and Valencia orange leaves are considerably greater than those of Eureka lemon leaves. In view of these differences, it would be logical to assume that differences would be found to exist in the freezing point lowerings of the expressed leaf sap, provided that carbohydrates are left out of consideration. It is the primary purpose of this paper to show the differences in the freezing point lowering of lemon and orange leaf sap. In addition to these fundamental physical differences between the leaf sap of lemon and that of orange, there are also chemical differences of considerable interest.

KELLEY and CUMMINS (4) have shown that the composition of the inorganic constituents of the ash of mature leaves is fairly constant in comparison with that of immature leaves, hence our studies were confined to normal leaves of one or more years of age, collected from 10-year-old trees growing on the grounds of the Citrus Experiment Station, Riverside, California. For each sampling one orange and one lemon tree growing in close proximity were selected.

It is generally recognized that the time of taking leaf samples for freezing point determinations is of utmost importance. This applies equally well to bark of shoots, as shown by HALMA (2). For this reason the leaves were collected on the shady side of the trees at approximately the same time, never later than 9:30 A.M.. This procedure minimized the effects of sunlight on the concentration of the leaf sap, a point which will be discussed in a later paper.

The leaves were wiped free from dust, frozen for approximately 20 hours, and then ground in a meat chopper. The sap was expressed with a hand press. Realizing that the amount of pressure applied in

[1] Paper no. 177, University of California Graduate School of Tropical Agriculture and Citrus Experiment Station, Riverside, California.

obtaining the sap is an important factor, great care was taken to apply as uniform a pressure as possible to all samples. The errors which might have resulted from this source are negligible when considered in comparison with the large differences obtained. The freezing point of the sap was determined with the Beckmann apparatus, and corrected for under-cooling by the formula given by HARRIS and GORTNER (3). Determinations were made as rapidly as possible, and any remaining portion of the sap was used for the determina-

TABLE I

FREEZING-POINT LOWERING (Δ) OF EXPRESSED LEAF SAP

DATE 1927	EUREKA LEMON	NAVEL ORANGE	VALENCIA ORANGE
	Δ	Δ	Δ
August 16	1.331	1.446	1.402
August 19	1.298	1.471	1.496
August 25	1.283	1.469	1.437
August 30	1.239	1.531	1.437
September 13	1.387	.....	1.631
September 16	1.359	.....	1.801
September 20	1.317	.....	1.727
September 23	1.327	.....	1.694
September 26*	1.160	.....	1.566
October 13	1.334	.....	1.498
November 3	1.187	.....	1.397

* Mature leaves of current season's growth from same trees as samples of September 20.

tion of ash, calcium, and magnesium by methods previously used by HAAS (1).

Table I shows that there are inherent differences in the physical characteristics in the sap of lemon and orange leaves. The lemon leaf sap was always more dilute than either Valencia or Navel orange, the smallest difference being 0.071° and the largest 0.442°. It will also be noted that there are no large or consistent differences between the values obtained for the Navel and Valencia saps, hence the investigation was largely confined to Valencia leaf sap. The absolute values obtained for the freezing point lowerings are by no means constant, but the important point to consider is that the values obtained for the two species always vary in the same direction and the difference is usually rather large. The results are especially

significant when it is considered that each determination represents samples from individual trees, and not a composite sample from many trees. It may be mentioned in passing that one of the factors which influences sap concentration is soil moisture; for example, after irrigation the sap tends to become more dilute. It is of interest in this connection to note that McCool and Millar (5, 6) found that the concentration of the soil solution is indicated by the freezing point lowerings of the root tissue, but found the tops to be far less sensitive to changes in concentration of soil solution. Their work

TABLE II

Inorganic constituents of 30 cc. of leaf sap, expressed in grams

Date 1927	Eureka lemon			Navel orange			Valencia orange		
	Ash	Calcium	Magnesium	Ash	Calcium	Magnesium	Ash	Calcium	Magnesium
August 16	1.4923	0.4502	0.1027	1.6394	0.5070	0.0622	1.8774	0.6243	0.0669
August 19	1.3753	0.4155	0.0888	1.7065	0.5385	0.0635	2.0688	0.7068	0.0704
August 23	1.5753	0.4661	0.1163	1.8929	0.5872	0.0767	1.9957	0.6578	0.0720
August 25	1.5115	.....	.....	.....	.....	.....	2.1926	.....	.....
August 30	1.4373	0.4414	0.0956	1.8459	0.6056	0.0652	2.0630	0.7138	0.0716

was confined to annuals, however, and hence may not be applicable to evergreen trees.

The amounts of ash, calcium, and magnesium found in the leaf saps used in table I are given in table II. It is significant that the ash and calcium content of the sap of the lemon leaves are always lower than those of the orange leaves, a fact which confirms the results presented in table I. It may be pointed out in this connection that the ash and calcium content (table II) of Valencia leaf sap is consistently greater than that of the Navel orange. In this respect the data secured from finely ground dried leaf material differ from those obtained from sap extracts. An additional point of interest is the fact that the magnesium content of lemon leaf sap is higher than that of sap of orange leaves; in other words, an inverse relationship exists as compared with the calcium content. A possible significance of this difference in sap-soluble magnesium will be considered in another paper.

Webber and others (8) have recorded the well known fact that

lemon trees are more susceptible to injury by freezing temperatures than orange trees. The data presented in tables I and II suggest an explanation for this phenomenon. The sap of lemon leaves, being more dilute, would naturally permit the leaves to freeze at a temperature at which the orange leaves would not be injured, provided the trees are growing under similar environmental conditions. Moreover, the sap concentration of leaves taken from the shady side more nearly represents the sap concentration of the leaves at night, the time when low temperatures generally occur. As pointed out by SWINGLE and ROBINSON (7), the kumquat (*Fortunella*) is one of the hardiest of evergreen citrous fruit trees. Limited data actually show that its leaf sap is more concentrated than that of the Valencia. Discussion of the effect of environmental conditions upon the freezing point lowering of leaf sap in citrus must await future investigation.

Summary

Fundamental differences exist in the freezing point lowering and in the ash, calcium, and magnesium content of leaf sap of Eureka lemon as compared with Valencia and Washington Navel orange. The sap of normal mature lemon leaves is less active osmotically and contains less ash and calcium, but more magnesium, than the sap of orange leaves. The fact that the sap of the lemon leaf is more dilute than that of the orange leaf furnishes a partial explanation of the differences in degree of sensitiveness to low temperatures between lemon and orange trees.

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BRIEFER ARTICLES

NOTE ON THE DECOMPOSITION OF SODIUM CYANIDE

During some recent investigations on the effect of various herbicides on plants, the writer performed some experiments with sodium cyanide to determine the rate at which it decomposed under various conditions. The results may be of interest, in view of the fact that the injurious after-effect of sorghum has been attributed to the formation of hydrocyanic acid by the sorghum residue. Sodium cyanide and hydrocyanic acid ought to decompose at approximately equal rates. When sodium cyanide is dissolved in water it hydrolyzes, forming hydrocyanic acid and sodium hydroxide. Such a solution has a very alkaline reaction. The reaction of a N/10 solution of sodium cyanide was calculated to pH 11.75.

Hydrocyanic acid and cyanides are described in textbooks of chemistry as unstable. By boiling an aqueous solution of potassium cyanide ammonium formate is formed. CLARK[1] found that a 24 per cent solution of potassium cyanide kept in the dark lost 75 per cent of its toxic value in ten days. BRENCHLEY,[2] growing barley seedlings in solutions containing 2.5 parts per million of hydrocyanic acid, found the plants to overcome the poisonous action of the solution after about 4 weeks. This may be interpreted as a disappearance of the poison by that time. HAWKINS[3] found solutions of potassium cyanide toxic in concentrations of 1.0 ppm. At a concentration of 0.5 ppm, some plants were stimulated, however, which may be a result of decomposition of the salt. PETIT[4] found that small applications of various cyanogen compounds increased the yields of plants in pot cultures.

When a solution, corresponding to 100 ppm of sodium cyanide, was added to soil in pots in which barley, oats, or Canada thistles were growing, the plants were killed over night or in a few days. If the application was made some days before the seeds were planted, however, the seedlings grew better in the treated soil than in checks, indicating not only a rapid decomposition of the cyanide but that its nitrogen content had been

[1] CLARK, J. F., On the toxic effect of deleterious agents on the germination and development of certain filamentous fungi. BOT. GAZ. **28**:289–327; 378–404. 1899.

[2] BRENCHLEY, W. E., Organic plant poisons. I. Hydrocyanic acid. Ann. Botany **31**:447–456. 1917.

[3] HAWKINS, R. S., Hydrocyanic acid as a toxic agent for plant growth. Jour. Amer. Soc. Agron. **17**:169–171. 1925.

[4] PETIT, A., Influence sur la vegetation de quelques composes cyanogenes. Jour. Agric. Pract. N.S. **45**:490–491. 1926.

made available for the plants. This observation prompted further investigation.

Several experiments were conducted in order to test certain factors that influence decomposition of NaCN. One of these was to test the influence of temperature on the decomposition of this salt. N/10 solutions were kept in darkness at 10°, 20°, and 30° C. for 40 days. Samples were withdrawn at regular intervals, and analyzed by titration with silver nitrate according to the Official Methods.[5] No decomposition of the salt was found in any of the samples. At the same time and under similar conditions, 200 cc. N/10 solutions was added to 100 gm. portions of soil in 300 cc. Erlenmeyer flasks. Aliquot samples were analyzed, at first daily and later at prolonged intervals. It was found that the concentration of the solutions, irrespective of temperature, decreased to about N/14 in 5 days. Later no changes took place up to 40 days, the time of the experiment. This result suggests that the cyanide was absorbed or adsorbed by the soil to a certain extent, but that no decomposition took place in a solution in contact with soil.

In order to test the decomposition under more natural conditions, solutions of sodium cyanide were added to 100 gm. portions of soil in amounts of 200 ppm of dry soil. Enough water was added to bring the soil to optimum moisture content. The samples were then kept at 10°, 20°, and 30° C. Daily one sample for each temperature was analyzed for cyanides. Two hundred cc. of water was added and the soil stirred. By suction through Buchner funnels fitted with three filter papers, clear solutions were obtained, which were titrated with silver nitrate. Soil samples kept at 10° C. gave a weak test for cyanide after 24 hours. Later analyses, as well as all analyses of samples kept at higher temperatures, gave negative results. The decomposition of the cyanide seemed to be very rapid. Finally sodium cyanide was added to soil in amounts from 50 to 200 ppm and barley sown immediately. It germinated in three days and made better growth in the treated than in the untreated soil. Thus the decomposition of sodium cyanide in soils is very rapid under "natural" conditions.

Since sodium cyanide decomposes so rapidly in soil, but not at all in a N/10 solution having a reaction of pH 11.75, it indicates that the decomposition is brought about by microorganisms.

It is not likely that a compound decomposing as rapidly as hydrocyanic acid is the cause of the injurious after-effect of sorghum.—ALFRED ASLANDER, *Cornell University, Ithaca N.Y.*

[*Accepted for publication December 2, 1927*]

[5] DOOLITTLE, R. E., ET AL., Official and tentative methods of analysis, etc. 2d ed. pp. 535. Washington.

CURRENT LITERATURE

BOOK REVIEWS

Symbionticism and origin of species

A new theory of the evolutionary origin of species is proposed by WALLIN,[1] who has for some years believed that mitochondria should be interpreted as symbiotic bacteria. The introductory chapter discusses the three cardinal features of evolution: the origin of species, the survival of species, and the direction of evolution. DARWIN'S principle accounts for the preservation of suitable organisms, but does not account for the production of evolutionary variations. The author of this book thinks that symbionticism does account for the evolutionary development of new species.

In the second chapter he discusses the history of mitochondrial research, from ALTMANN'S original work in 1890 to the present time, and then proceeds to a discussion of the bacterial nature of the mitochondrial bodies. This theory rests upon staining reactions in part, upon reactions to physical and chemical agents, upon thermal responses, and upon cultural studies made with tissues. The main cultural studies were made with liver tissue from new born or fetal rabbits, explanted to a rabbit liver meat infusion medium. Pieces of fat, kidney, and suprarenal tissue from rabbits, guinea pigs, dogs, and cats were used also, with the production of growths which lead WALLIN to state: "These facts, apparently, admit of no other interpretation than that mitochondria are living organisms, symbiotically combined with the cells of plants and animals." That is a large conclusion to draw from about ten pages of discussion, which contains only a small amount of experimental evidence. The foundation seems to the reviewer too thin to bear the weight of superstructure that rests upon it.

Chapter IV takes up the behavior of mitochondria, pleomorphism, transformation into glandular secretions, experimental modifications, relation to disease, to cell division, and neoplastic growths. The author takes these activities as those of symbiotic bacteria, and proceeds to define symbionticism in the following chapter.

This term he defines as an "absolute intracellular symbiosis" resulting from positive prototaxis. In the author's words: "Mitochondria represent one of the symbionts in the expression of a positive prototaxis resulting in an absolute symbiosis. The universal presence of mitochondria in the cells of all plants and animals constitutes evidence that the development of such relationships is not

[1] WALLIN, I. E., Symbionticism and the origin of species. 8vo. pp. xii+171. Baltimore: Williams and Wilkins. 1927.

a digression from normal biological behavior, but rather the result of a fundamental principle. The universality of positive prototaxis resulting in absolute symbiosis, or symbionticism, forces us to recognize this as of fundamental importance. Just as reproduction insures the *perpetuation of existing species*, the author believes that *symbionticism insures the origin of new species*."

The sixth chapter deals with some cases of known microsymbiosis. Included among these are such forms as *Amoeba viridis*, sponges, *Hydra viridis* and other *Coelenterata*, turbellarian worms, and other forms inhabited by such algae as the *Zoochlorellae*, *Zooxanthellae*, etc. Cases of bacterial microsymbiosis include *Pelomyxa vivipara* among the Protozoa; such insects as *Blatta germanica*, *Periplaneta orientalis*, *Camponotus ligniperda*, *Formica fusca;* and certain bioluminescent animals, such as squids, whose luminiferous organs contain luminescent bacteria.

Chapter VII analyzes the symbiont relations, and then the author attempts to show that symbionticism is responsible for the origin of species. The final paragraph of chapter VIII expresses WALLIN'S convictions. "It appears to the author that symbionticism offers a rational explanation for many of the variations in the morphology and physiology of plants and animals. When these variations are of sufficient magnitude and permanence, they constitute new species. The facts that mitochondria are universally present in the cells of all organisms higher than the bacteria, that mitochondria are bacterial in nature, and that microsymbiosis can determine morphologic and physiologic changes in organs and cells, can lead to no conclusion other than that *symbionticism is a fundamental causative factor in the origin of species*."

The last two chapters consider the relation of symbionticism to heredity and development, and to organic evolution in general. WALLIN tries to fit his theory to the existing theory of Mendelian behavior. Rejecting the idea that evolution is due to the loss or disintegration of genes, but must be accounted for by the acquisition of new genes, he proposes the idea that the acquisition of a new symbiont in the cells of an organism may be the means by which new genes are added to the germ cells. The actual formation of the gene is pictured as the transfer of the chromatin material of the bacterial symbiont to the germplasm of the host. That is, on entering the cell, the chromatin scattered through the bacterial body is supposed to leave it and pass to the chromatic material of the host cell nucleus. The bacterial body, with its chromatin gone, remains in the cytoplasm, and becomes by subsequent divisions the mitochondria of the host cell cytoplasm. In the nucleus of the host cell, the chromatin of bacterial origin is supposed to take its place in the chromosome as a new gene, and to enter upon the expression of new characters on its own account. Also, by modification of other genes already present, the new gene may have many complex effects in the realm of hereditary variations.

The final chapter leaves one unsatisfied, because there is lacking anything concrete in the application of symbionticism to the actual evolution of life upon the earth. It merely gives the author an opportunity to emphasize the difficul-

ties of all theories to explain the origin and direction of the evolution of higher organisms.

The work presents a unique point of view, very insufficiently supported. Many able scientists have studied the mitochondria without catching this view of their significance. If WALLIN were to be found correct in his interpretation, the work would open up many excellent lines of research. It takes a man of courage to publish a theory which he knows will be by some rudely discarded, and made by others the center of hot controversy in which he may be worsted. The discussion is interesting, and even if it is unconvincing, it should gain for its author a respectful hearing. The very lack of convincingness may stimulate work on the part of those who do not agree with WALLIN'S interpretation, to the end that proof of the correctness or incorrectness of the basic observations may be brought forward. It should be relatively easy to determine whether the evidence of chapter III is valid.—C. A. SHULL.

Biochemical laboratory methods

At the time of his death, the late Professor MORROW[2] of the University of Minnesota left an unfinished manuscript of a laboratory manual of biochemical methods, which has been brought to completion through the efforts of Mrs. MORROW, with the assistance of Dr. R. A. GORTNER and T. A. PASCOE of the Division of Agricultural Biochemistry. The book is designed particularly for students of the biological sciences, and it seems to the reviewer a satisfactory manual, particularly for the non-medical groups.

The experiments cover a wide range of procedures, and anyone who masters the technique outlined in this work will be well grounded in the fundamentals of biochemical methods. There are 233 experiments outlined, which are grouped into nine chapters. The first deals with the colloidal state, and offers 65 studies of dialysis, diffusion, osmosis, optical properties of colloidal matter, preparation of sols, emulsions and emulsoids, electrical properties, ultra-filtration, viscosity, surface tension, surface energy, adsorption, and related topics.

Chapter II presents several exercises on the physical chemical constants of plant saps, and the following chapter considers the measurement of hydrogen-ion concentration, and buffer phenomena. The fourth chapter deals with the proteins, and offers forty valuable experiments which lead up to the analysis of a protein for its principal nitrogen fractions. The following chapter gives thorough consideration to the carbohydrates. Thirty-six of the exercises deal with the soluble monosaccharides and disaccharides, and twenty with the polysaccharides.

The four remaining chapters are less extensive, and treat the glucosides, fats and allied substances, enzymes, and plant pigments. The enzyme experiments cover the proteases and amidases, carbohydrases, glucosidases, esterases, oxidases, and catalase.

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[2] MORROW, C. A., Biochemical laboratory methods. 8vo. pp. xviii+350. New York: Wiley and Sons. 1927.

Literature citations accompany the experimental directions, and provide a satisfactory background of biochemical theory for the student's work. A book of this kind has long been needed; it should find wide use among those preparing for physiological and biochemical research.—C. A. SHULL.

Factors controlling germination and early survival in oaks

A study of the problems connected with germination of oaks and the early survival of seedlings of the various species of *Quercus* has been made by KORSTIAN,[3] of the Appalachian Forest Experiment Station. The study included conditions of successful storage, factors influencing the germination, such as biotic factors, moisture conditions, temperature, pericarp difficulties, character of food reserves, size of seeds, and certain soil conditions, like compactness of surface, and the influence of leaf litter on the retention of soil moisture and on the retention of viability of the seeds.

The loss of seeds through the ravages of insects, and the agency of rodents and other animals, is very large, 50–100 per cent in some cases. Retention of viability depends partly upon retention of water in the seeds. Red oak acorns are slightly drier than those of the white oak, the usual percentage of water being 50–60 per cent for the former, and 60–70 per cent for the latter species. If the acorns dry out there is a large decrease in viability by the time the moisture content reaches 20–30 per cent, and complete loss if the water content falls as low as 10–15 per cent. Proper storage must provide sufficient atmospheric or soil moisture to maintain the general high level of water content in the seeds, and at the same time provide enough oxygen for the respiration of the moist acorns.

The most favorable temperature in general is 50–65° F., low at night and higher in the day time. Below 40° germination does not occur, and at 80–95° night and day temperature, the temperature affects the germination unfavorably.

There is some delay of germination among the black oak group, a group whose seeds are more fatty than those of the white oak group. The presence of a rest period, and high-temperature hastening of germination, is believed to be associated with enzyme activity, particularly with reference to the conversion of fats to carbohydrates.

Forest fires usually destroy the viability of acorns lying under the leaf litter. The species or groups differ in their resistance, the red oak acorns being most resistant. In order of decreasing resistance to high temperature, the groups stand as follows: red oak, chestnut, black, scarlet, and white. As in many other cases, the larger acorns give more vigorous seedlings and better percentage of germination than the smaller seeds.

One of the edaphic factors of importance is the compactness of the surface soil. Studies of the soil with a penetrometer, coupled with studies of the ability

[3] KORSTIAN, C. F., Factors controlling germination and early survival in oaks. Yale Univ. School Forestry, Bull. 19. pp. 115. New Haven. 1927.

of the oak seedlings to penetrate the substratum, lead to the conclusion that the limit of soil penetration for oak radicles occurs with a surface penetrability of 0.01–0.023 mm. per gram of load applied.

Leaf litter is of the greatest importance in producing an environment suitable to germination and survival, because it stabilizes the moisture and temperature conditions, and prevents compacting of the surface soil beyond the limits of root power of penetration.

It is a pleasure to see forestry research turning toward the more fundamental physiological problems of tree life. There must be a much stronger movement in this direction if forestry is to become something else than a superficial branch of botanical science.—C. A. SHULL.

Physical chemistry and biophysics

An attractive textbook on physical chemistry and biophysics for students of the biological and medical sciences has been prepared by STEEL.[4] It is well written, intensely interesting, and more practical than most books of the kind. It gives exactly the kind of information that students need for an understanding of the fundamental physical chemistry of cellular physiology.

The book contains thirteen chapters, the first of which is a brief introduction outlining the background of the modern development of physical chemistry in the service of biology. Chapter II considers the nature and structure of matter, atomic theory and recent advances in knowledge of atomic structure, radiations, radioactive substances, isotopes, atomic numbers and X-ray spectra, the laws of chemical reactions, etc. This is followed by a chapter on the general properties of matter, states of aggregation, gas laws, and deviations in behavior, liquids, viscosity and fluidity, crystalline state, and crystal systems.

The fourth chapter considers the energy transformations in living matter with reference to the laws of thermodynamics. The storage of potential energy in living matter, the energy changes of photosynthesis, and energy changes in animals are some of the topics discussed. Chapters V–VIII take up the general nature of solutions, water as a solvent, diffusion and osmotic pressure, and the nature and behavior of electrolytes in solution. The discussion of osmotic pressure is somewhat meager, but few exceptions can be taken to the statements made.

The later chapters take up the problems of chemical equilibrium and the law of mass action in physiological processes, measurement of hydrogen-ion concentration, colloidal state of matter, catalysis and the velocity of chemical reactions, and the dynamical physical chemistry of the cell. The chapter on the colloidal state is by far the longest in the book, and is a valuable treatment of the subject for the student.

The reviewer considers this book one of the best of its kind. It is worthy of

[4] STEEL, M., Physical chemistry and biophysics. 8vo. pp. x+372. New York: John Wiley and Sons. 1928.

a place on the young biologist's five-foot bookshelf. Even those who are not specializing in physiological fields would do well to know this book. The capacity to carry on worth-while investigations in any biological field will be enlarged by possession of the information presented in such a book.—C. A. SHULL.

Flora of the Panama Canal Zone

STANDLEY[5] has published a very important contribution to our knowledge of the flora of the Panama Canal region. In 1921 the governor of the Canal Zone asked the assistance of the Department of Agriculture in the preparation of an illustrated flora of the region. STANDLEY was selected to prepare the flora, and the results of his investigations are now published. The purpose of the investigation was not only to contribute to our scientific knowledge of the region, but also to develop our knowledge of tropical agriculture. Some idea of the method of presentation may be obtained from the statement that "with the aid of the many English and Spanish common names, it should not be difficult for the casual visitor to identify most of the important plants of the Canal Zone."

The flowering plants of the region number about 2000 species. Besides the native plants, the keys include also the cultivated species. The work is based on the collections of the United States National Herbarium, which for many years has been receiving a wealth of material from collectors. STANDLEY himself visited the Canal Zone twice, studying the flora and making collections. He gave special attention to the common names in use, and also to the local uses of plants. The publication is not merely a taxonomic account of the flora, therefore, but includes also much material of more general interest.

An interesting account is given of the contrasts in physiography and flora of the Atlantic and Pacific slopes. About two-thirds of the Canal Zone lies on the Atlantic slope, and has a highly diversified flora, very little of the pioneer vegetation remaining. The Pacific slope is comparatively arid, and the vegetation is very different in type from that of the Atlantic slope. This difference in the two floras consists not only in the general appearance, but also in the genera and species represented. The most conspicuous element of the Atlantic slope flora is the great number and variety of palms. The author also includes a very interesting account of the history of botanical exploration in Panama. In short, the publication assembles in a single volume all of the available information in reference to the development of our knowledge of a very interesting region. It will also make it possible to appreciate and investigate more intelligently the closeness of the relationship of this flora to that of South America. The 66 remarkably fine plates picture some of the outstanding features of the flora.

Only about 50 pages are taken up with the general presentation of the

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[5] STANDLEY, PAUL C., Flora of the Panama Canal Zone. Contrib. U.S. Nat. Herb. **27**: pp. 416. *pls. 66.* 1928.

region, its history and its outstanding features. The bulk of the volume is made up of the taxonomic presentation of the flora, and presents the facts in simple and readable form. Detailed descriptions are not given, but there are keys for identification that will help the taxonomist. These keys include not only all the native or naturalized species, but most of the introduced plants grown for ornament or for economic purposes. In the case of the more important plants, those likely to prove of the greatest interest to the public, more extensive accounts are given which will assist in recognizing the species. It is not a rigidly taxonomic work in the usual sense, therefore, but a general introduction to the flora of an interesting region, which may be of service not only to botanists, but also to all who may be interested in the region.—J. M. C.

Flora of the Chicago region

In spite of the fact that for more than quarter of a century Chicago has been a center of botanical research, the region has been without any adequate check list until the present volume by PEPOON.[6] This is much more than a check list, as it contains many things besides an annotated list of more than 1900 of the vascular plants of the region. The 115 illustrations serve to enliven the text and assist in the recognition of many species. This recognition is further aided by 25 simple keys for groups and families. These include one for the trees in winter condition, illustrated with pen-and-ink sketches of 50 twigs and buds.

The recent geological history of the region is sketched, and on a topographic and ecologic basis six distinct floral districts are outlined. Each of these is mapped and its vegetation discussed in a separate chapter. This furnishes a historical background of the original plant associations that will be of permanent value. The good printing and binding, the excellent photographs, well produced, the careful organization, and the adequate index all add to the value of the book.—G. D. FULLER.

Investigations on chlorophyll

This classic work by WILLSTÄTTER and STOLL has been translated into English by SCHERTZ and MERZ,[7] both of the United States Department of Agriculture. The translation is fairly faithful, and many students will be pleased to use the work in this form. It is too well known to need description, but has not been well enough known to those who might want to make use of the methods WILLSTÄTTER developed. The price of the book is $4.50, and can be obtained only from Dr. F. M. Schertz, 1305 Farragut St. N.W., Washington, D.C.—C. A. SHULL.

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[6] PEPOON, H. S., An annotated flora of the Chicago region. Chicago Acad. Sci. Bull. Nat. Hist. Survey **8**: pp. xxii+554. *figs. 115. 7 maps.* 1927. $3.50.

[7] SCHERTZ, F. M., and MERZ, A. R., Investigations on chlorophyll. WILLSTÄTTER and STOLL. 8vo. pp. xii+385. Science Press Printing Co., Lancaster, Pa. 1928.

NOTES FOR STUDENTS

Taxonomic notes.—KECK[8] has published a revision of *Orthocarpus*, which restricts the genus to the annuals, the longer-lived ones being incorporated in *Castilleja*. In addition to the ordinary enumeration of species, the author has constructed a suggestive phylogeny, illustrated by a chart. The genus as defined includes 25 species and 23 varieties, 4 of the latter being new.

BROTHERUS[9] has published an account of the known species of the mosses of Hawaii. The number of representatives of this group, both in species and genera, is remarkable. There are 84 genera recognized, including 139 species, 45 of which are described as new.

HENRARD,[10] in continuation of his revision of *Aristida*, which is a preliminary study to a monograph, has presented and discussed 168 species, 24 of which are described as new. There are many changes in nomenclature, and some of the species include numerous varieties. The species are presented in alphabetical order, the present paper extending from *A. hassleri* to *A. prodigiosa*. This will give some indication of the size of the genus.

MAIDEN[11] has published two additional parts of his revision of *Eucalyptus*. The first paper deals with *E. bloxsomei*, a new species, and presents in great detail its distribution and the factors that influence it, the problem of age and area, etc. In the second paper 10 species are discussed, followed by many details relating to the effective study of *Eucalyptus*, and its importance in numerous phases of industry and education.

PRAIN and BURKILL[12] have published an account of a collection of species of *Dioscorea* obtained from Siam. The species are said to belong to various floras that meet in Siam. The paper contains descriptions of 32 species, in 6 sections of the genus, 8 of which are described as new. There are also 6 new varieties.

SMALL[13] has described a new palm, *Sabal jamesiana*, discovered in the Everglades of Florida. He calls attention to the fact that Florida may well be called the "land of palms," since 13 of the 16 species occurring in the United States are found there.

---

[8] KECK, D. D., A revision of the genus *Orthocarpus*. Proc. Calif. Acad. Sci. **16**:517–571. 1927.

[9] BROTHERUS, V. F., Hawaiian mosses. Bernice P. Bishop Museum, Bull. 40. pp. 37. *pls. 8*. 1927.

[10] HENRARD, J. T., A critical revision of the genus *Aristida*. Mededeelinger Van's Rijks Herb. Leiden. no. 54A. 221–464. 1927.

[11] MAIDEN, J. H., A critical revision of the genus *Eucalyptus*. Vol. VII. part 7. Publ. by Government of New South Wales, Sydney, Australia. 1926. Vol. VII. part 8. *ibid*. 1927.

[12] PRAIN, D., and BURKILL, I. H., The genus *Dioscorea* in Siam. Kew Bull. no. 6. 1927.

[13] SMALL, J. K., The James Palmetto, *Sabal jamesiana*. Jour. N.Y. Bot. Gard. **28**:181–185. 1927.

BLAKE[14] has published a new revision of *Diplostephium*, the former one having been published in 1922. It was called for by the securing of new material and information. The genus is closely related to *Aster*, and the author regards it as "an Andean development of *Aster*." It is a South American genus, with the center of its abundance in Colombia. The new revision includes 43 species, 7 of which are described as new.

KOBUSKI[15] has described a new genus (*Apassalus*) of Acanthaceae. It includes three species separated from *Dyschoriste*. These species occur in Haiti and Santo Domingo, Cuba, and southeastern United States.

KOBUSKI[16] has published a monograph of the American species of *Dyschoriste*, based upon a study of the material contained in the principal American herbaria. Preceding the description of the species, he presents an account of the history, the general morphology, the geographical distribution, and the phylogeny of the genus. The recognized species are 40 in number, 12 of which are described as new. There is also a full record of all the specimens examined.

Miss MATHIAS,[17] in beginning the publication of her studies of the Umbelliferae, has presented a full account of the maritime genus *Glehnia*, disentangling it from its previous taxonomic treatment. Two species are recognized, which are closely related, but they occur along the coast on both sides of the Pacific. One species extends from Alaska to northern California, and the other from Siberia to southern China and through Japan.

In continuation of his studies of the Fabaceae, RYDBERG[18] has presented the genus *Atelophragma*. This genus was established in 1906, based on 6 species of *Astragalus*. In the present paper 22 species are recognized, distributed through 7 sections. Six species are described as new, and 8 are transferred from other genera. In another paper[19] he continues his presentation of the genus, describing 21 species, seven of which are new. The total number of species he has now published in the genus is 46.

RYDBERG[20] has also published some of the results of his investigation of *Psoraleae*, a tribe of Fabaceae. He characterizes 19 genera in the key, and gives an account of the first 8 of them in the present paper.

---

[14] BLAKE, S. F., Review of the genus *Diplostephium*. Amer. Jour. Bot. **15**:43–64. 1928.

[15] KOBUSKI, C. E., A new genus of Acanthaceae. Ann. Mo. Bot. Gard. **15**:1–8. 1928.

[16] ———, A monograph of the American species of the genus *Dyschoriste*. Ann. Mo. Bot. Gard. **15**:9–90. 1928.

[17] MATHIAS, MILDRED E., Studies in the Umbelliferae I. Ann. Mo. Bot. Gard. **15**:91–108. 1928.

[18] RYDBERG, P. A., Notes on Fabaceae. X. Bull. Torr. Bot. Club **55**:119–132. 1928.

[19] ———, Notes on Fabaceae. XI. Bull. Torr. Bot. Club **55**:155–174. 1928.

[20] ———, Genera of North American Fabaceae. III. Tribe Psoraleae. Amer. Jour. Bot. **15**:195–203. 1928.

RUSBY[21] has published a new genus (*Mulfordia*) of Zingiberaceae from the marsh region of Bolivia. Only a single specimen was collected, which at first was thought to belong to *Costus*.

TRELEASE[22] has published 4 new species of *Peperomia* from Bolivia. OSTERHOUT[23] has described 3 new species from Colorado, belonging to the following genera: *Quamoclidion*, *Astragalus*, and *Townsendia*.

Miss DREW[24] has published a revision of a group of small filamentous Rhodophyceae on the Pacific Coast. The discussion of the relationships shows that the species of *Chantransia* and *Acrochaetium* should be referred to *Rhodochorton*. Under that generic name she describes 34 species, among which there are 18 new species, 11 new combinations, and one new variety.

BLAKE[25] has described 12 new species of Compositae from Mexico and some of the northern countries of South America. They include 4 species of *Verbesina*, 2 of *Gynoxys*, and 1 each in 6 other genera.

SPRAGUE[26] has described a new genus (*Diacrodon*) of Rubiaceae from Brazil, from specimens that were assigned originally to the genus *Borreria*. It belongs to the tribe Spermacoceae, and seems to be a very distinct genus.

MUNZ[27] has published a revision of *Chylismia*, a subgenus of *Oenothera*, based on his study of the collections in many herbaria. Eight species are recognized, and 14 varieties, 3 of the latter being described as new. Some idea of the complexities of the group may be obtained from the fact that there are 6 new names for varieties, and 4 new combinations. The descriptions are very complete, and all the known collections are cited.

MUNZ[28] has published an elaborate revision of *Antirrhinum* and related genera, as represented in the "New World." The descriptions are very full, and all the localities from which material has been obtained are noted. Seven genera

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[21] RUSBY, H. H., *Mulfordia*, a new genus of the Zingiberaceae. Bull. Torr. Bot. Club **55**:165, 166. 1928.

[22] TRELEASE, WILLIAM, New species of *Peperomia* from Bolivia. Bull. Torr. Bot. Club **55**:169–170. 1928.

[23] OSTERHOUT, G. E., New plants from Colorado. Bull. Torr. Bot. Club **55**:75, 76. 1928.

[24] DREW, KATHLEEN M., A revision of the genera *Chantransia*, *Rhodochorton*, and *Acrochaetium*. Bot. Publ. Univ. Calif. **14**:139–224. 1928.

[25] BLAKE, S. F., Twelve new American Asteraceae. Jour. Wash. Acad. Sci. **18**:25–37. 1928.

[26] SPRAGUE, T. A., *Diacrodon*, a new genus of Rubiaceae from Brazil. Kew Bull. Miscell. Inf. no. 1. 32–34. 1928.

[27] MUNZ, P. A., A revision of the subgenus *Chylismia* of the genus *Oenothera*. Amer. Jour. Bot. **15**:223–240. 1928.

[28] ———, The Antirrhinoideae-Antirrhineae of the New World. Proc. Calif. Acad. Sci. **15**:323–397. 1926.

are included, one of which (*Epixiphium*) is new. The species are 45 in number, the large genera being *Linaria* (15 species) and *Antirrhinum* (14 species).—J. M. C.

Hydrogen ion concentration of certain western American inland waters.—SHELFORD[29] has reached the conclusion that hydrogen ion concentration is related to salt content of the water and to the amount of decomposition of organic matter. The bicarbonates are usually the measure of buffer value, but this is influenced somewhat by other alkaline salts. The decomposition of organic matter, respiration of organisms, etc., yield H_2CO_3. A water with much buffer will neutralize the CO_2 from the decomposition and respiration of many organisms and still remain alkaline. A water with little buffer would become acid under the same conditions. Heavy rains of rainy periods in dry and moderately rainy regions and of regions of heavy rainfalls increase the hydrogen ions by diluting the buffer.

Where two streams meet, as the Columbia and Snake rivers of this study, differences in condition are due to age of waters, etc. With two waters of unequal age, four or more differences occur: in hydrogen ions, in temperature, and in quantity and quality of dissolved content. The effects of hydrogen ion concentration on the distribution of animal life in the water are modified by the amount of oxygen, quality of salts, etc., dissolved in the water.

There are two principal difficulties involved in hydrogen ion determination under the conditions of this investigation; one is the loss of CO_2 due to contact with the air, and the other is the failure to get the sample from the place where the organisms in question live.—J. ISENBARGER.

North American Flora.—The first part of volume 23 contains the beginning of a presentation of the Mimosaceae by N. L. BRITTON and J. N. ROSE, including the Ingeae, the first of the six tribes. It contains 16 genera, all but the last one (*Lysiloma*) being presented. The following new genera are described: *Jubunba* (from *Acacia*) with 15 species, *Punjuba* (from *Pithecolobium*) with 1 species, *Cojoba* (from *Mimosa*) with 17 species, *Painteria* (from *Pithecolobium*) with 4 species, *Chloroleucon* (from *Pithecolobium*) with 9 species, and *Pseudalbizzia* (from *Acacia*) with 1 species. Much the largest genus is *Anneslia*, with 113 species, 46 of which are described as new. Distributed among the other genera are 28 new species.—J. M. C.

---

[29] SHELFORD, V. E., The hydrogen ion concentration of certain western American inland waters. Ecology **6**:279–287. 1925.

GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold-face** type; synonyms in *italics*.

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